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A LITERATURE REVIEW AND ANNOTATED BIBLIOGRAPHY

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WOLVERINE (*Gulo gulo*)

BIOLOGY AND MANAGEMENT:

A LITERATURE REVIEW
AND
ANNOTATED BIBLIOGRAPHY

Prepared for The U.S. Forest Service

Northern Region :
Threatened, Endangered, and Sensitive Program

By: Thomas W. Butts

September, 1992

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ACKNOWLEDGEMENTS

This document was prepared for the INTERAGENCY LYNX-WOLVERINE-FISHER WORKING GROUP that was formed in late 1991 to address concerns regarding the status and management of the lynx, the wolverine, and the fisher in the United States south of Canada, and to coordinate efforts between various federal and state agencies and private individuals working with these species.

The primary funding for this project was provided by the United States Forest Service Northern Region Threatened, Endangered, and Sensitive Species Program, under the direction of Bill Ruediger. The Wildlife Division of the Montana Department of Fish, Wildlife, and Parks provided additional funding to complete the project.

Assistance in tracking down references was provided in part by Dave Genter of the Montana Natural Heritage Program, and numerous very helpful individuals at the Heritage Program and at the State Library. Editing assistance was provided by Dave Genter, and by Pat Farmer of Western Technology and Engineering, Inc. (WESTECH), of Helena, MT. Nancy Horn assisted by patiently answering my numerous word-processing questions. Michelle Brown did the cover illustration and helped with a number of details necessary to complete the project. My sincere thanks to all of these individuals and any I may have overlooked.

PART I WOLVERINE BIOLOGY AND MANAGEMENT SUMMARY

INTRODUCTION

This document presents a bibliography of current literature on the wolverine (*Gulo gulo*), and summarizes information on its biology and management. Surprisingly, much of the available wolverine literature concerns only certain topics such as reproduction, status surveys, and collections of anecdotes. Apparently only four intensive ecological field surveys of the wolverine have been done to date in North America, one each in Montana and the Yukon, and two in Alaska. There is a sizable body of work on the wolverine from Russia, Norway, and Sweden. However, since this document's primary emphasis is wolverine management in the United States south of Canada, the priority for review and inclusion was: first literature concerning wolverines in this area; second on literature concerning wolverines in Canada and Alaska; and third, on work deemed particularly relevant from the Old World.

The literature review was conducted using several computer data bases such as BIOSIS, the U.S. Fish and Wildlife Reference Service database, the Montana State Library, and the libraries at the University of Montana in Missoula and Montana State University in Bozeman. In addition, letters requesting current or recent information were sent to Wildlife Cooperative Research Units, state wildlife agencies, Canadian provincial ministries of environment, and state Natural Heritage Programs in all states and Canadian provinces where wolverines occur.

TAXONOMY

Scientific nomenclature

The New and Old World wolverines are currently considered one circumpolar species, *Gulo gulo*. Kurten and Rausch (1959) suggested that the wolverine is a relatively recent arrival in the New World, perhaps arriving late in the Pleistocene, because New World specimens differ little from Old World wolverines. They nominated *Gulo gulo gulo* for Old World and *Gulo gulo luscus* for New World wolverines. Banci (1982b) found that differences between the Vancouver Island wolverine and mainland wolverines were insufficient to warrant a separate subspecies, thus suggesting a monotypic, continent-wide species.

Common names

The wolverine has been called glutton, devil bear, skunk bear, devil beast, and carcajou.

DISTRIBUTION

Old World wolverines are found from Scandinavia east across the forest-tundra and taiga of Eastern Europe and Asia (Kvam et al.1984, Wilson 1982). Historically, North American wolverines were distributed widely across the northern part of the continent, including most of Canada and the northern tier of states in the continental U.S., and southward along the Rocky Mountains to Arizona and New Mexico at higher elevations (Hash 1987). Hall (1981) recorded historical occurrence in California, Oregon, Washington, Idaho, Montana, Utah, Wyoming, Colorado, New Mexico, North Dakota, South Dakota, Nebraska, Minnesota, Wisconsin, Michigan, Illinois, Indiana, Pennsylvania, New York, Vermont, New Hampshire, and Maine. Mead and Mead (1989) recorded a wolverine from a cave in Nevada that probably dates from the late Pleistocene, 16,000 to 13,000 years B.P.

Current distribution is considerably reduced. In Canada, Van Zyll de Jong (1975) reports that wolverines have become "quite rare and restricted in distribution" east of the prairies (see also Prescott 1983), are common only in the extreme northern edge of the prairie provinces, and in British Columbia and the Territories. They are still common in Alaska, but Montana harbors the only widespread population in the lower 48 states (Hash 1987). They were apparently almost extinct in Montana by 1920 but recovered through dispersal from Canada and Glacier National Park (Newby and Wright 1955, Newby and McDougal 1964). Occasional sightings have been made in California (Kovach 1981, Ruth 1954, Yocum 1973), Colorado (Nead et al. 1984), Idaho (Bachman et al. 1990, Groves 1987, Pengelly 1951), Oregon (Yocum 1973), Utah (McKay 1991), Washington (Johnson 1977, Yocum 1973), and Wyoming (Hoak et al. 1982). Wolverines may be on the comeback in several western states, primarily due to the reduction of the use of poisons placed in carcasses to control predators, and dispersal from Canada (Wilson 1982, Hatler 1989). Clark et al. (1989) state that wolverine populations have never made much of a recovery in the Greater Yellowstone Ecosystem (including Yellowstone National Park and environs) since being nearly extirpated in the early 1900's.

Preliminary distribution maps for the wolverine have been prepared by a committee of the Interagency Lynx/Wolverine/Fisher Working Group (Figures 2 - 9). Figure 1 is a cover letter for these distribution maps citing references and other information used to develop these preliminary maps. Note that the overall strategy for compiling the maps was to draw a line around all records, both current and historical, irrespective of verification, from Natural Heritage Program data bases, state records, and other published distribution data.

A revised version of these maps is currently (1992) being prepared by the committee that will distinguish between current data (1982-1992) and historic data (1981 or older) that will use only verified and probable sighting records.

Figure 1. Cover letter.

Wolverine/Fisher/Lynx
Summary of Distribution Information

April 1, 1992
Prepared by M.Maj and Dr. Oz Garton

The following is a summary of information that went into the development of the distribution maps (preliminary) of the wolverine, lynx and fisher for the states of California, Colorado, Idaho, Montana, Oregon, Utah, Washington and Wyoming. The following summary is presented by individual states and species.
The overall strategy was to broadly draw a line around all individual records provided from Natural Heritage Data bases, State records and published data and depict as distribution. No differentiation of historic versus current records were made. All records were used irrespective of their verification.

The next version of distirbution maps will distinguish between current data (1982-1992) and historic data (1981-older). Only verified and probable siting records will be used. Sign such as tracks and scat will not be used. Enclosed is a version of the new distribution maps, fisher distribution in Oregon.

Total records; 1,001 wolverine records, 434 lynx records and 273 fisher records. totally 1608.

CALIFORNIA

Wolverine: Ron Schlorff of the California Department of Fish and Game provided 278 records dating from 1893 to the present. Diane MacFarlane of the USDA Forest Service provided 89 additional records from observations on Forest Service lands dating from 1974 to the present.

COLORADO

Wolverine: Historical records of wolverine are scarce and thus the animal is not thought to have been common in Colorado (Nead et.al., 1985). Examination of 265 reports of wolverines were rated as: 3 positive reports, 18 probable, 36 possible and 208 non-wolverine reports (Nead et.al., 1985). The distribution map presented is from Nead, Halfpenny and Bissell, 1985. The 57 records classified as

IDAHO

Information used for the Idaho distribution maos came from GAP analysis information made available from University of Idaho. Species records and data from the Natural Heritage Program database was used in the GAP map.. Dr. Oz Garton of University of Idaho produced the 3 species distribution maps for Idaho. Point records, range is interpretation of sites where location records occurred. Interpretation by Craig Groves and other Idaho State Fish and Game folks.

MONTANA

The information for all three species was interpreted from "Distribution of Montana Amphibians, Reptiles and Mammals; Preliminary Mapping by Latilong." by Larry S. Thompson, 1982. The information on species occurence is given by latilong. This information was modified by integrating information on the layout of public lands and mountain ranges.

Wolverine: Additional records were retrieved from the State trapping records.

OREGON

Records are all fromNatural Heritage Program.

Wolverine:81 records; 1 record in 1912 the rest from 1960-1991

WASHINGTON

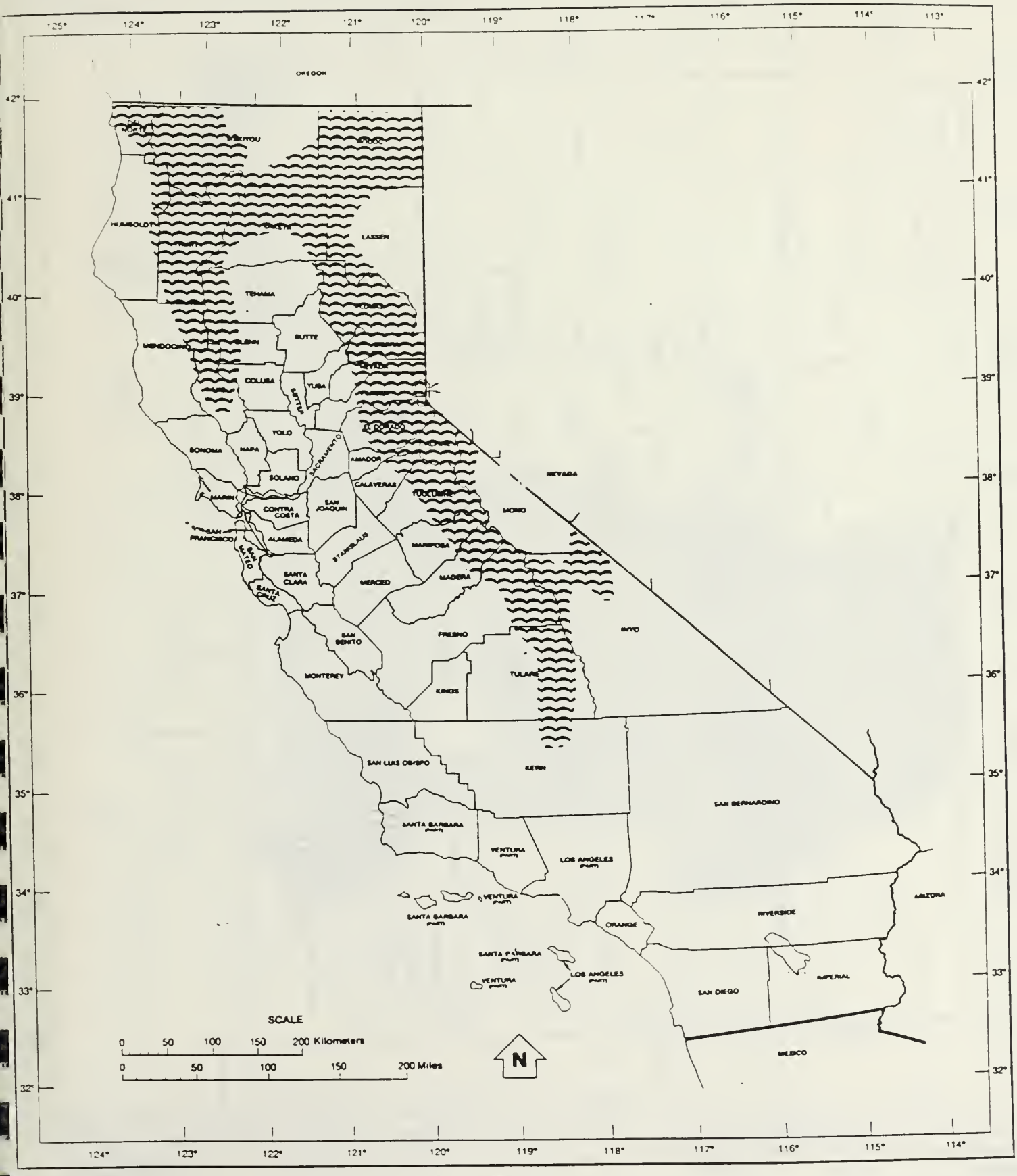
Wolverine: Natural Heritage records; 90 records

WYOMING

Wolverine:108 Natural Heritage records

WOLVERINE DISTRIBUTION

Counties



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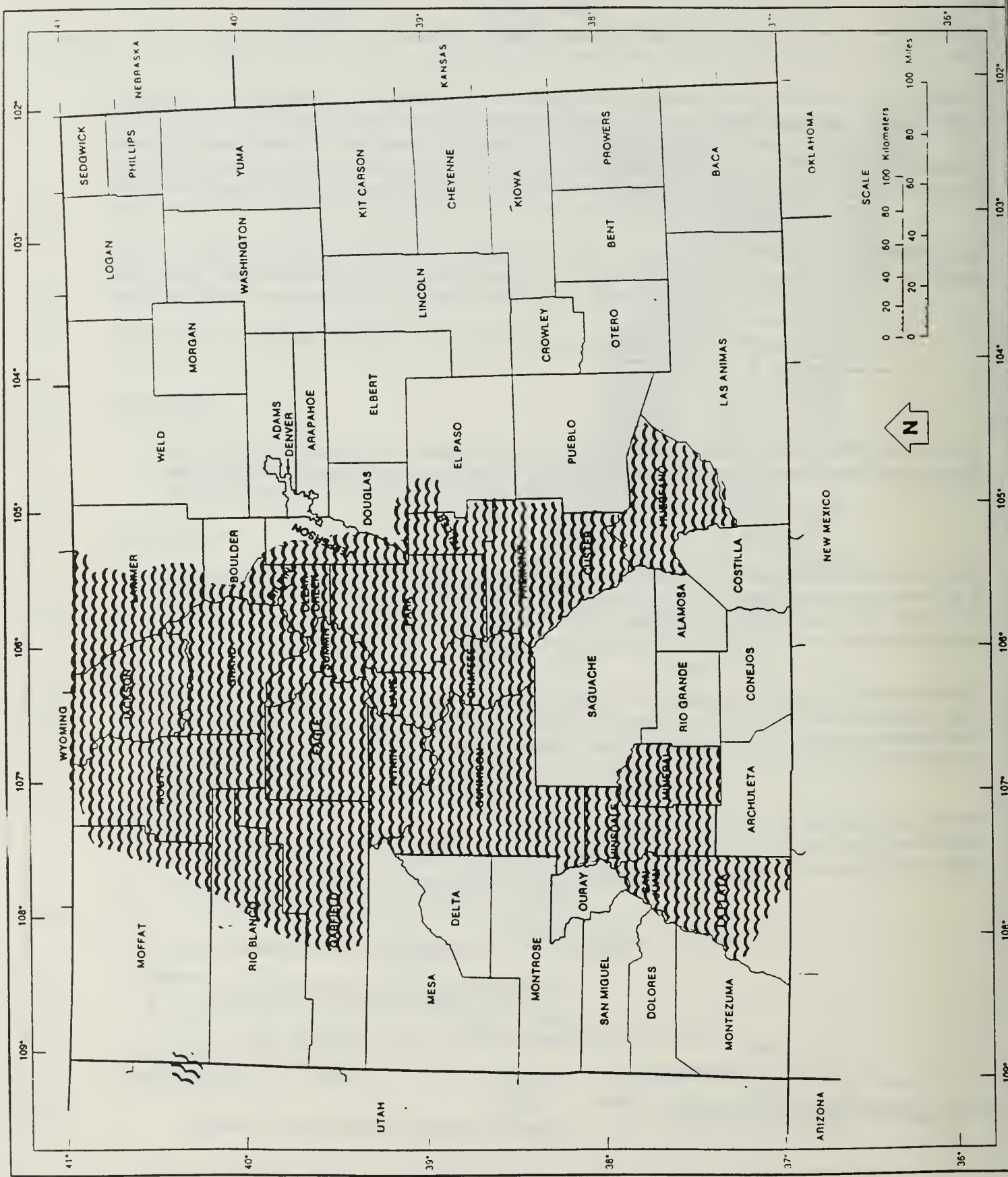
MAPS

Figure 2. CALIFORNIA

WOLVERINE DISTRIBUTION

Counties



U.S. DEPARTMENT OF COMMERCE Economics and Statistics Administration Bureau of the Census

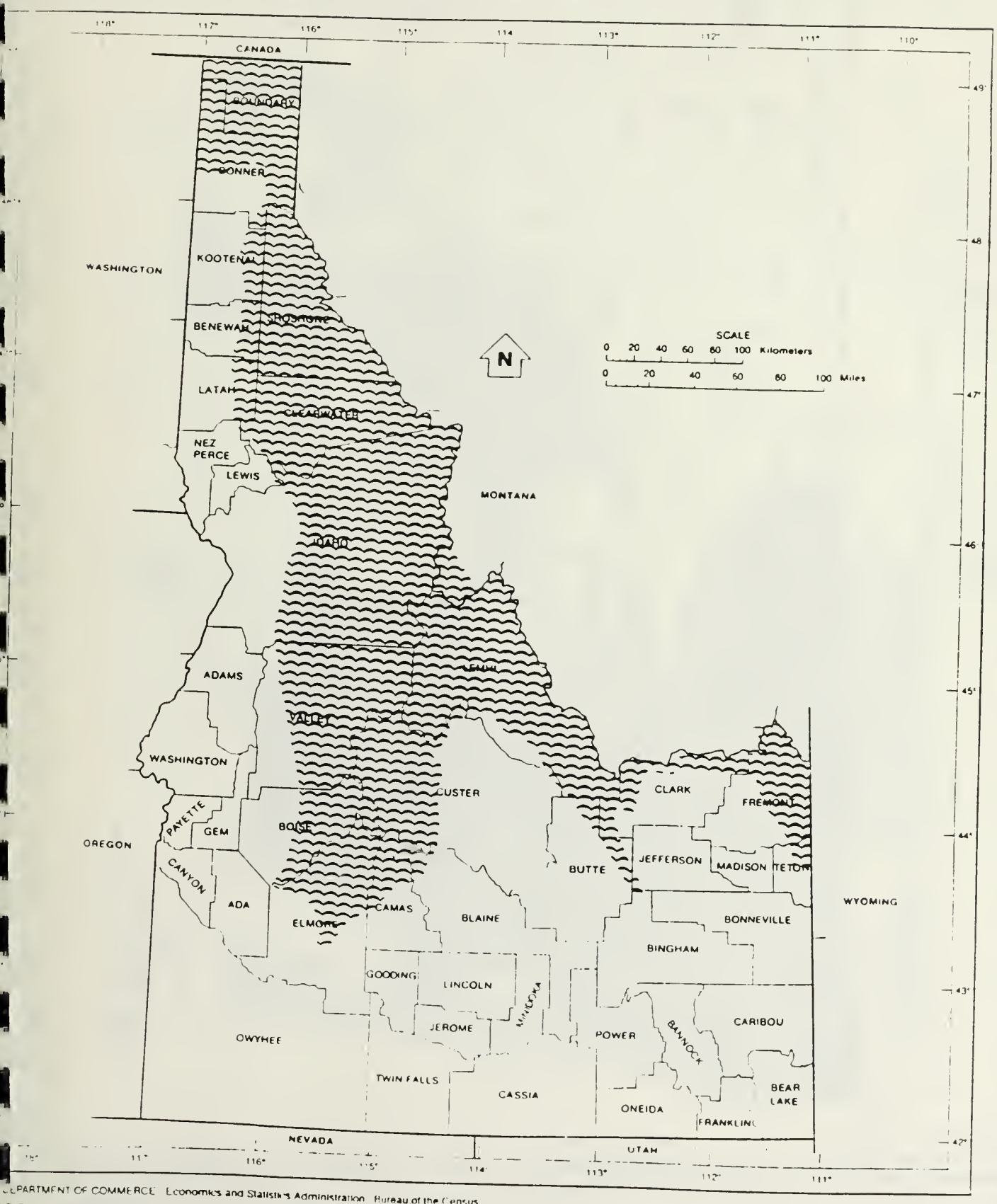
MAPS

Figure 3.

COLORADO

WOLVERINE DISTRIBUTION

Counties



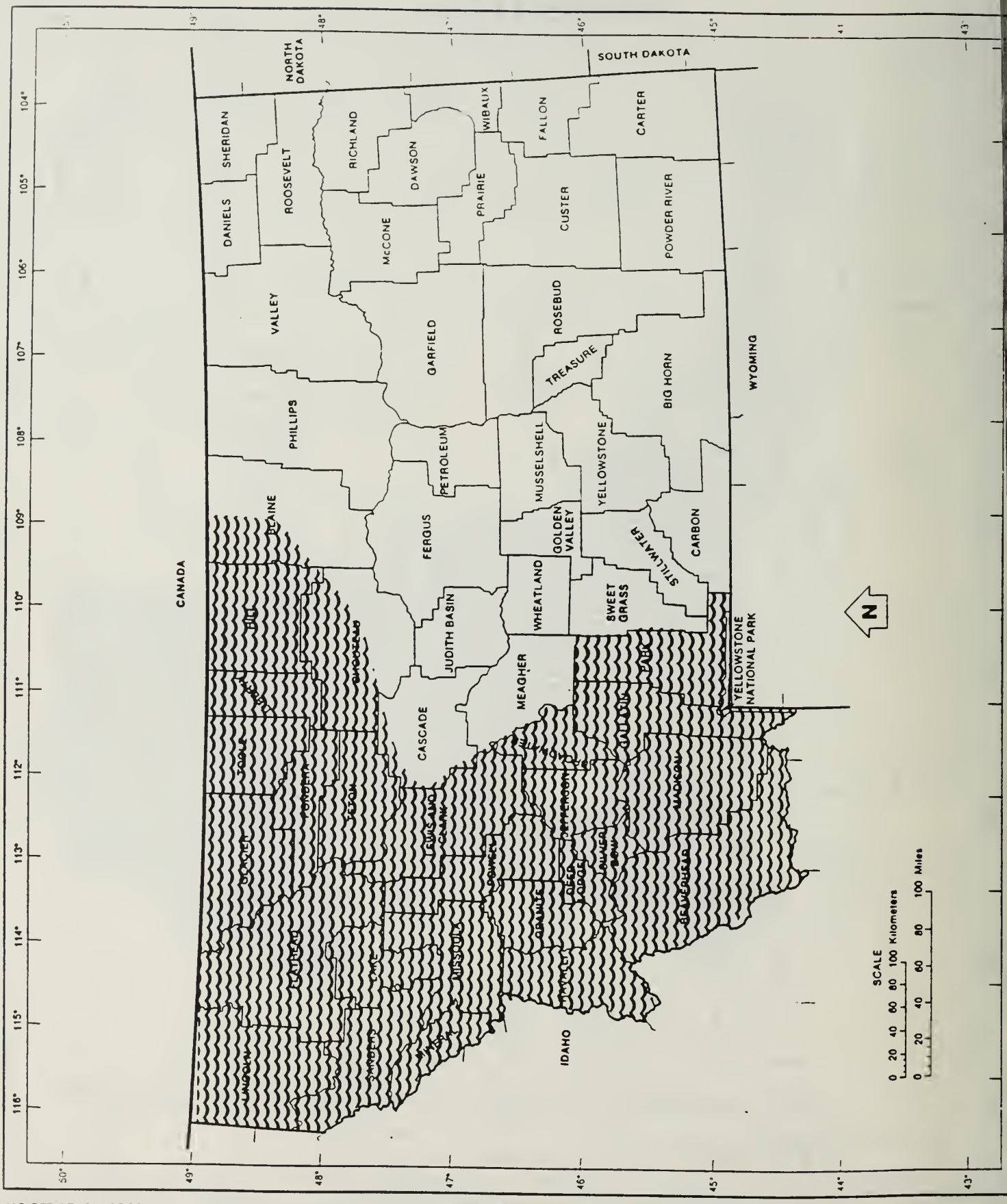
DEPARTMENT OF COMMERCE Economics and Statistics Administration Bureau of the Census

MAPS

Figure 4. IDAHO

WOLVERINE DISTRIBUTION

Counties



U.S. DEPARTMENT OF COMMERCE Economics and Statistics Administration Bureau of the Census

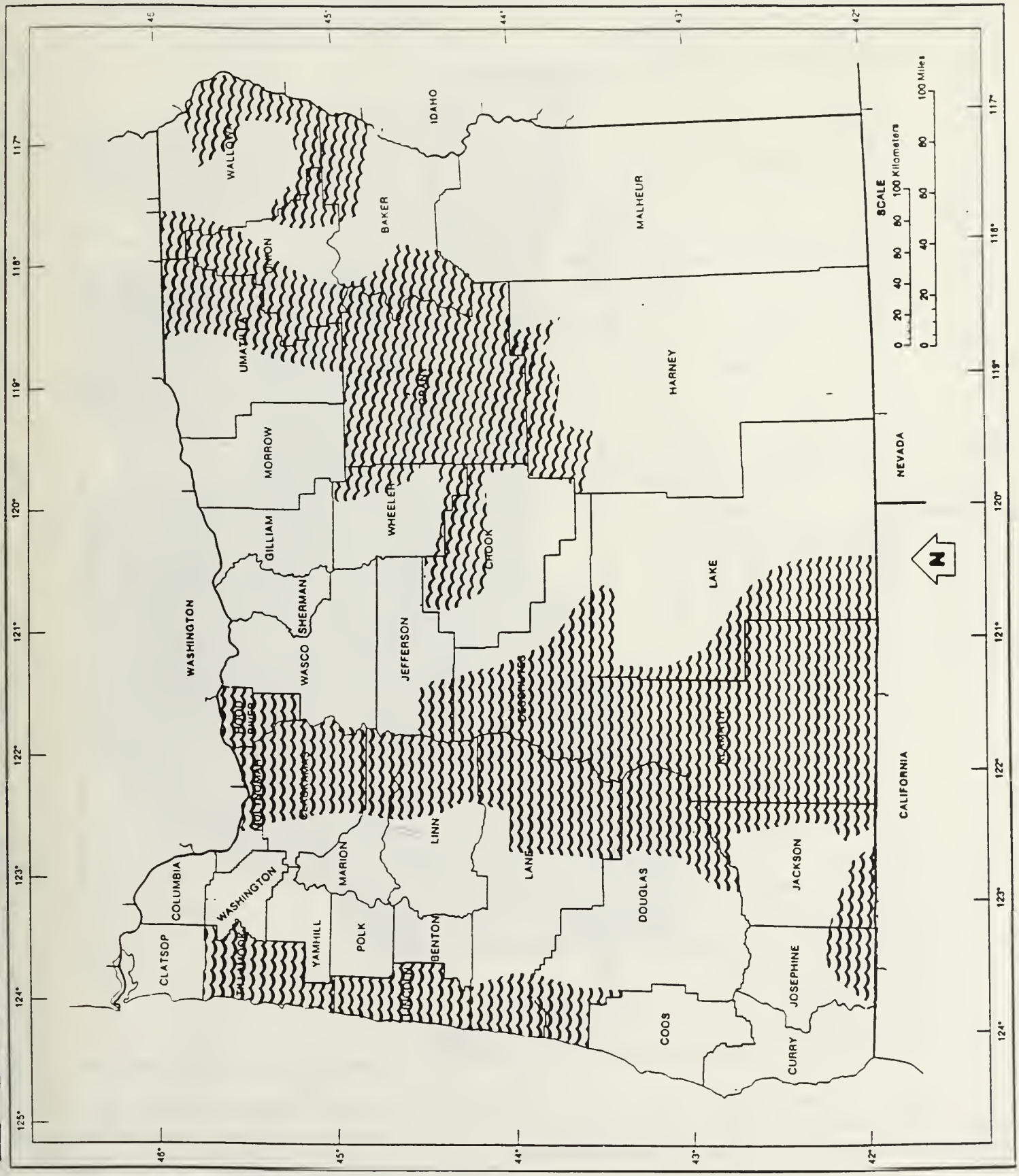
MAPS

Figure 5.

MONTANA

WOLVERINE DISTRIBUTION

Counties



U.S. DEPARTMENT OF COMMERCE Economics and Statistics Administration Bureau of the Census

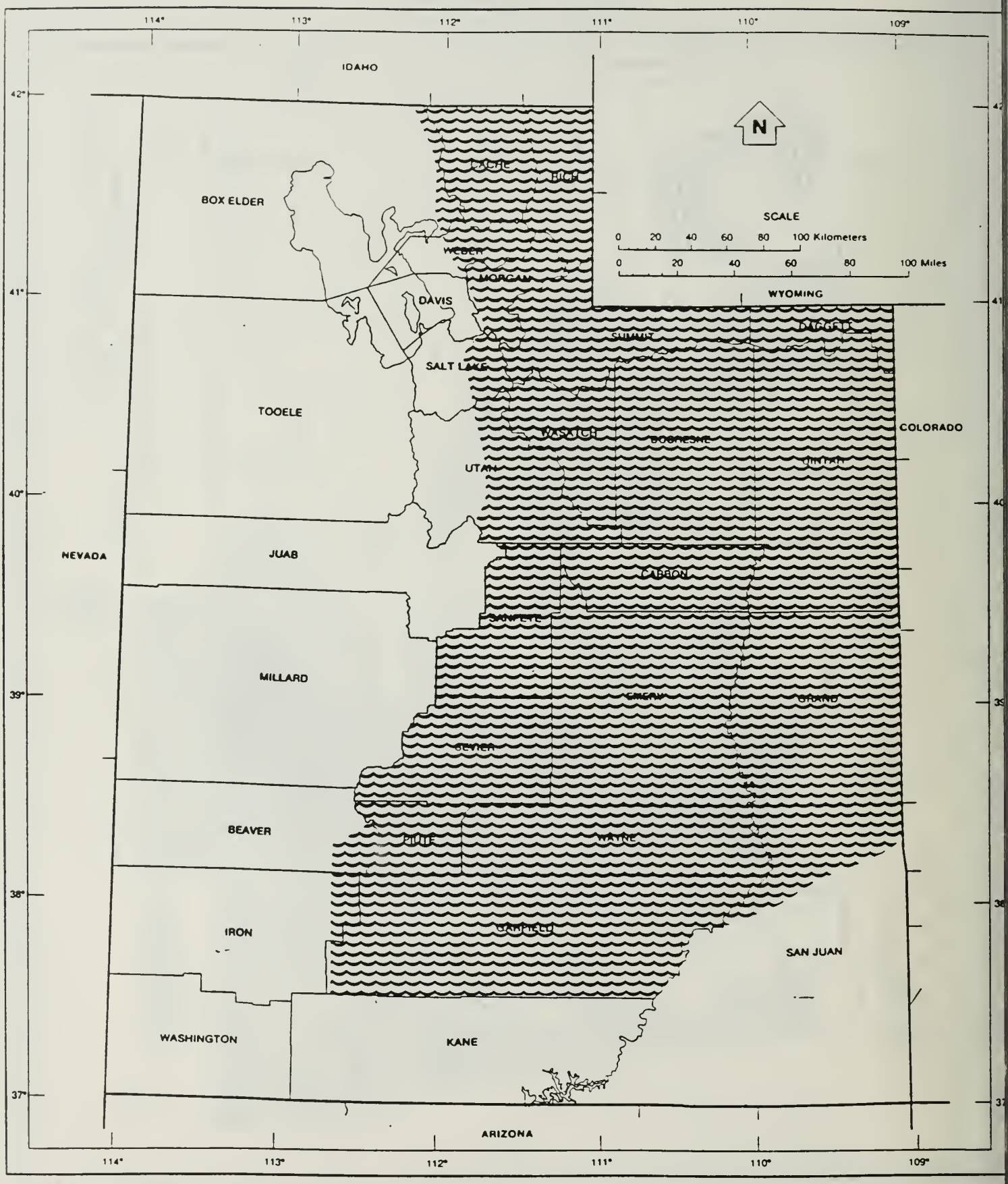
MAPS

Figure 6.

OREGON

WOLVERINE DISTRIBUTION

Counties



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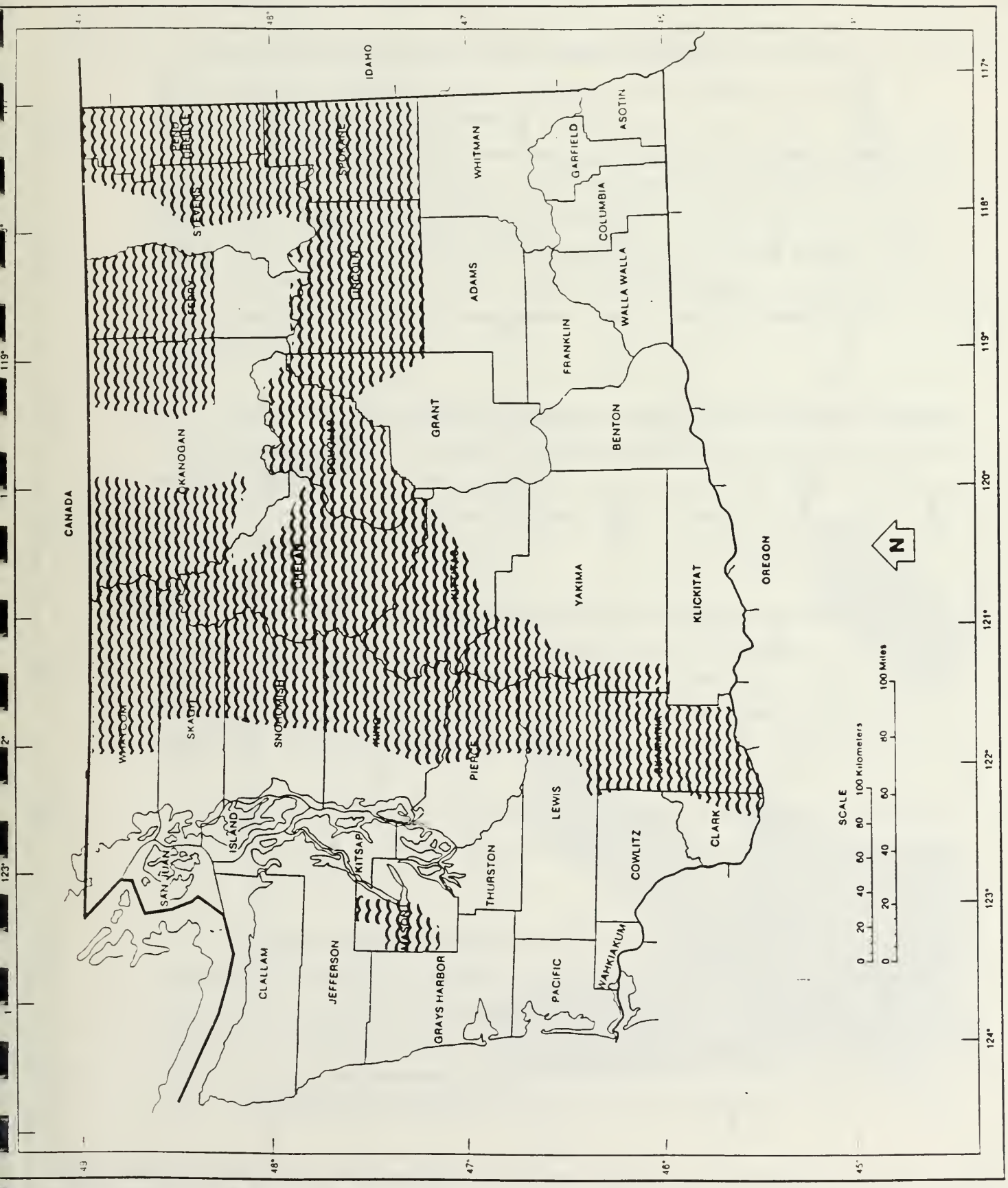
MAPS

Figure 7... UTAH

WOLVERINE DISTRIBUTION

ounties



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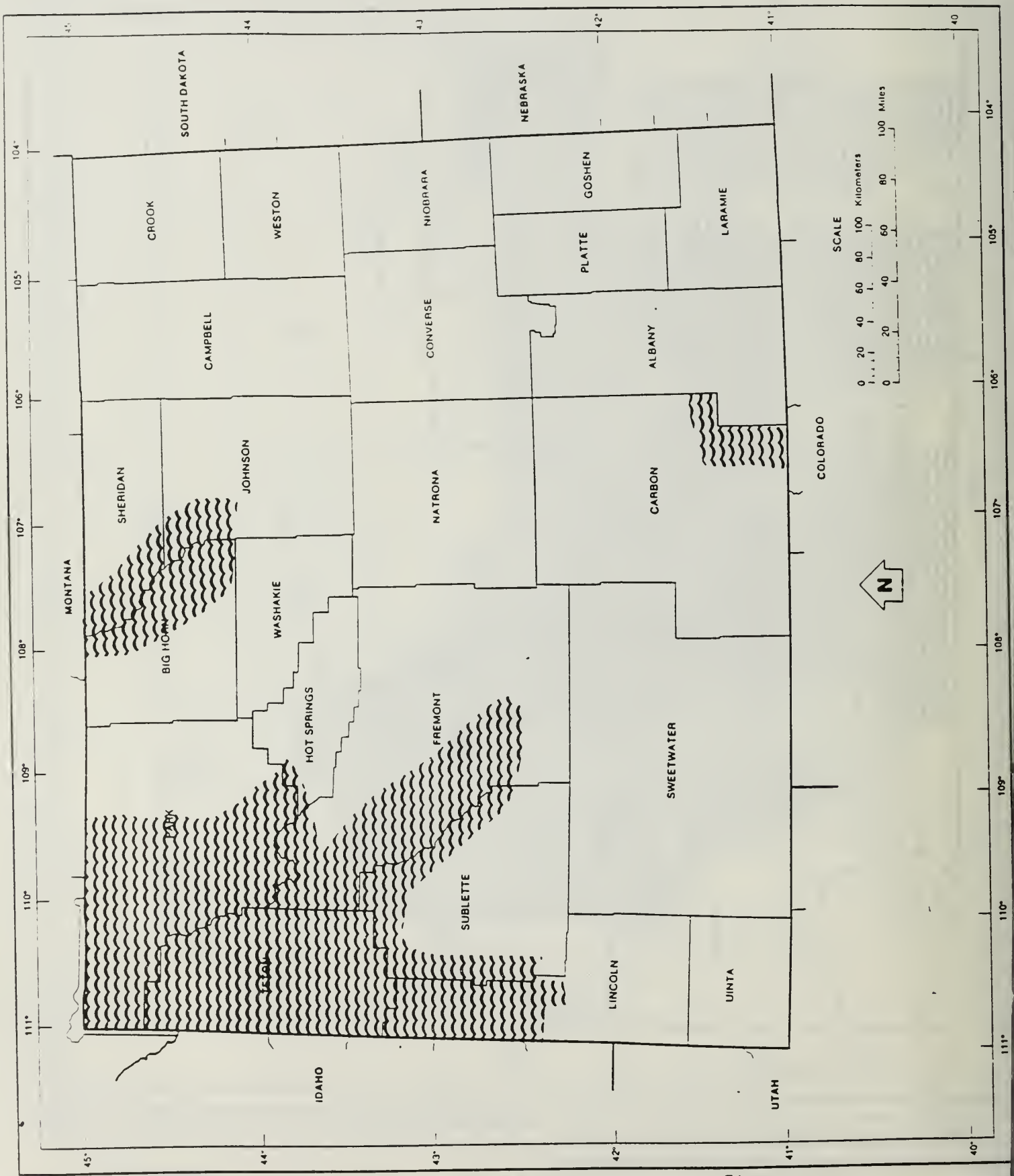
APS

Figure 8. WASHINGTON

WOLVERINE DISTRIBUTION

Counties



U.S. DEPARTMENT OF COMMERCE Economics and Statistics Administration Bureau of the Census

Figure 9.

DESCRIPTION

The wolverine is one of the largest members of its family, the Mustelidae, and resembles skunks (*Mephitis*) and badgers (*Taxidea*) more than other members such as weasels (*Mustela* spp.) and otters (*Lutra* and *Enhydra*) (Wilson 1982). It has often been likened to a small bear with a bushy tail. Adults range in length from 65 to 105 cm (25 - 41 in.) from nose to rump, the tail adding another 17 to 26 cm (6 1/2 - 10 in.) (McKay 1991). It is compact and strongly built, with a short neck, a broad, flattened head with canidlike jaws, and relatively short legs. It carries its head and tail somewhat lower than its arched back, in a lumbering gait.

Wolverines are sexually dimorphic, the males averaging 30-40% heavier than females. Males in Eurasia and North America range in weight from 9 - 20 kg, averaging about 14 kg in the far north and about 12 kg in the southern portion of their range. Females range from 6 to 14 kg, averaging about 10 kg.

Hatler (1989) suggests that physical uniformity across their range may result from species mobility and wide-ranging dispersal, providing little opportunity for gene pool segregation. Therefore, Hatler (1989) concludes that wolverine study results from any one locale are probably applicable throughout their range.

The mean weight of 24 live-trapped research animals in a Montana study was 12.7 kg (28 pounds) for males and 8.3 kg (18 pounds) for females (Hornocker and Hash 1981).

The feet are large, with five toes and long (2-3 cm), sharply curved, semi-retractile claws. The hindfeet are slightly smaller than the forefeet. The third digit is longest on the hind feet while the fourth is longest on the forefeet (Wilson 1982, Hash 1987).

Tracks are variously described as from 7-12.5 cm (2.8-5 in.) wide

and 8-15 cm (3.2-6 in.) long (McKay 1991). Sometimes mistaken for wolf tracks, they are easily distinguished by the presence of the fifth toe, and the more crescent shaped pad (Murie 1974).

Wolverine pelage is composed of a wooly, dense underfur 2-3 cm long and coarse, stiff guardhairs 6-10 cm long. The fur is short and dense on the head and gets progressively longer posteriorly. The tail is particularly shaggy, with hairs 15-20 cm long. Wolverine pelts are valued for their rarity, their beauty and their ability to shed frost and ice (Quick 1952, Hash 1987).

Wolverines vary in color from brown to black, with a contrasting stripe, varying from blond to reddish brown, extending from the shoulder along the flank and joining across the rump. There is frequently a blond band on the face from ear to eye, and usually light-colored markings on the throat and chest (Wilson 1982, Hash 1987).

The sense of smell is well developed, allowing them to detect food over long distances. Hornocker and Hash (1981) reported wolverines were able to locate carrion under 1-2 m of snow. They have relatively small eyes and poor eyesight (Jackson 1961).

Anal musk glands, characteristic of all mustelidae, are located just inside the anal orifice, are about the size of a walnut, and emit a tannish brown, highly odiferous secretion (Hash 1987). Wolverines use boulders, small trees, and branches of larger trees as "marking sites", chewing and scratching bark and spraying with musk, apparently to advertise their presence.

Females have eight mammae; four abdominal and four inguinal (Jackson 1961). The dental formula is incisors 3/3, canines 1/1, premolars 4/4, molars 1/2 = 38 teeth (Wilson 1982).

(See pictures of wolverine skull and tracks in Jackson 1961, reprinted in Part III of this document).

LIFE HISTORY

Reproduction

The breeding season ranges from late spring to early fall, but most breeding occurs during early summer (Hash 1987, Wright and Rausch 1955). Magoun (1985) and Liskop et al. (1981) suggest that wolverine females are capable of breeding every year, though Ewer (1973) and Ingles (1965) reported that litters are produced only every two or three years.

Females carry the unimplanted blastocyst until the following December or January. After implantation, active gestation takes 30-40 days. Total gestation periods have been reported from 215 to 272 days (Hash 1987, Mehrer 1976, Wright and Rausch 1955).

From one to five kits, generally two or three, are born from February through April (Hash 1987). In British Columbia Liskop et al.(1981) found a mean litter size of 2.6 based on five reproductive tracts; Hornocker and Hash (1981) reported a mean of 2.2 embryos from a sample of six female wolverines in Montana.

Kits are born fully covered with white (sandy, or light buff: Jackson 1961, Rue 1981) fur, unopened eyes, and unerupted teeth (Mehrer 1976). The young grow rapidly, and are weaned beginning at 7-8 weeks (Myhre and Myrberget 1975). They leave the den at 12-14 weeks (Magoun 1985) and reach adult size by early winter (Rausch and Pearson 1972).

Mortality

Humans are the primary "enemy" of wolverines, though a few reports of wolverines killed by wolves exist (Burkholder 1962, Wilson 1982, Hatler 1989). Wilson also cites an account of a wolverine dying from the quills of a porcupine it had ingested, and Jackson (1961) states that this does happen on occasion.

It is likely that the wolverine's ecological niche as a seasonal scavenger predisposes it to a precarious existence. Banci (1981, 1987), Hornocker and Hash (1981), and Magoun (1985) all report either animals dead from starvation or in poor physical condition.

Hash (1987) summarized a number of reports of life expectancy. He reports that wild wolverines in Montana rarely exceed 8 years of age. Other studies he reviewed reported maximum longevities of 8-11 years for wild wolverines, and up to 18 for captives.

ECOLOGY

Habitat

Wolverines are found in a broad variety of habitats, but are generally associated with montane, forested areas. Eurasian wolverines utilize forest and tundra, in low mountains, or coniferous forests bordering high mountains, and swampy areas of northern coniferous forests (Krott 1960, Haglund 1966). Magoun (1985) studied a population of wolverines living in the arctic tundra of northwestern Alaska, while Gardner's (1985) Alaska study focused on wolverines in sparsely forested mountain habitats in southcentral part of the state. Habitats in western Canada and the western U.S. are generally coniferous montane forests of two types, as described by Hash (1987): " The Pacific coastal forest types dominate the wolverine's range along the coast from Washington to British Columbia and southern Alaska for approximately 150 km (93 miles) inland. The coastal composition is also present throughout interior Washington and the Idaho panhandle into extreme northwestern Montana. This forest complex is primarily composed of western white pines (*Pinus monticola*), lodgepole pines (*Pinus contorta*), ponderosa pines (*Pinus ponderosa*), grand firs (*Abies grandis*), Douglas firs (*Pseudotsuga menziesii*), western hemlocks (*Tsuga heterophylla*), Engelmann spruces (*Picea engelmannii*), red cedars (*Thuja plicata*), and western larches (*Larix occidentalis*). Stringers and groves of black cottonwoods (*Populus trichocarpa*) are present along the

lower parts of primary drainages. From south to north, and from lower to higher elevations, dominance generally shifts from the pine-fir to the spruce-alpine types."

"The Rocky Mountain forest types dominate the occupied wolverine range in Colorado, Montana, southwestern Alberta, and most of interior British Columbia (Bailey 1980). The primary species are the firs (*Abies* spp.), pines, and larches (*Larix* spp.). Most of the white pines, cedars (*Thuja* spp.), and hemlocks (*Tsuga* spp.) characteristic of the coastal types are absent. Trembling aspens (*Populus tremuloides*) are common along many slopes and cottonwoods are prevalent along most streams. Many ecotonal areas occur in conjunction with marshes, lakes, cliffs, transition zones between primary cover types, and elevation gradients that appear to be important habitat components. Wolverines prefer marshy areas (Wilson 1982)."

Hornocker and Hash (1981) reported that 70% of 576 radio-relocations of collared wolverines were " in medium or scattered mature timber, with a strong selection for forests featuring alpine fir, while the rest were primarily in ecotonal areas. Dense young timber, burns and wet meadows were rarely used, and there were no relocations in logging clearcuts." " ... animals occasionally crossed clearcuts, but usually in a straight line and at a running gait, as compared to more leisurely and meandering (hunting) patterns in timber. Bed sites were often in snow on open outcrops, but 'all in timber types which afforded cover.' A distinct seasonal elevational pattern was documented, with the wolverines occupying higher ranges during the snow-free season than in winter" (Hatler 1989).

Hatler (1989) stated there is no concrete evidence that wolverines are dependent upon a particular cover type, though forest cover may be important in some areas to escape predation by wolves. Banci (1986) states "habitat requirements appear to be large, isolated tracts of wilderness supporting a diverse prey base, rather than specific plant associations or topography."

Most sources reviewed for this document agreed with Groves' (1988) description of wolverine habitat south of the northern boreal forests as generally "large, mountainous, and essentially roadless areas" or Whitman et al.'s "rugged and inaccessible habitats", thus it is especially interesting that McKay (1991) reported a number of wolverine sightings " around the Skyline Drive area at the head of Ephraim Canyon, and in the Wasatch Mountains" of Utah, areas near fairly dense human populations that have both back country hiking and vehicle use. Hash (1987) states that, though wolverines are generally associated with back-country or wilderness areas, with little human disturbance, they do cross areas of human habitation, usually at night, during long-range travels.

Den sites have been well described. They are generally made in narrow defiles with a high concentration of fallen logs, or under tree roots or protruding rocks, in caves, or in burrows in overhanging banks, or in deep snow (Pulliainen 1968, Rue 1981, Hash 1987). Females will often den near a large winter-killed carcass to be utilized as a food source (Rausch and Pearson 1972, Rue 1981). Myberget (1968) found most dens located in Norway were in 3-5 meters of snow, next to cliff faces, in open areas with southern aspects. Snow appears to be a common denominator to most wolverine dens, with rocks or trees a frequent associate. "There does not appear to be any specific 'critical habitat' that can be identified for protection of denning opportunities" (Hatler 1989).

Home range

Because wolverines range widely over a considerable diversity of habitats, it is not surpeising that annual home ranges reported from North American studies vary considerably, but they are consistently large. Hornocker and Hash (1981) reported a mean annual home range size for nine Montana male wolverines of 422 km^2 (163 square miles). Studies in Alaska by Magoun (1985) and Whitman et al. (1986) reported larger home range sizes for males; 666 km^2 (257 sq. mi.) and 535 km^2

206 sq. mi.) respectively.

Lactating females in the Montana study had much smaller spring and summer ranges (100 km^2) than other females, whose average annual home range was 388 km^2 (159 square miles) (Hash 1987). Annual home ranges reported for females were about 100 km^2 in south-central Alaska (Whitman et al. 1986) and 70 km^2 in arctic Alaska (Magoun 1985).

Banci (1987) found a marked male wolverine in the Yukon had a smaller home range (238 km^2) than those in Alaska or Montana. Because other studies reported that male home ranges are generally larger than female's, and are larger in the summer than winter (Hash 1987), apparently because of breeding activity, Banci (1987) hypothesized that the male wolverine she studied had a particularly small home range (only 46 km^2 in summer) because he had easy access to food and three females.

Variability between methods and presentation of results in all North American wolverine studies, and food and mate availability, were mentioned by Banci (1987) as potential reasons for differences between reported annual and seasonal home ranges. As discussed by Hatler (1989), home range sizes are probably more indicative of food abundance, environmental conditions, and/or relative stability and density of local populations than any intrinsic characteristic of wolverines. Of importance to wildlife managers is that wolverines do exhibit some fidelity to particular areas for months or even years, that males generally have larger home ranges than females, and that females without kits have larger home ranges than those with young.

Daily movements

Numerous accounts reveal that the wolverine is a wanderer, capable of covering great distances in shorts period of time. For the purposes of this document, "daily movements" cover a wolverine's activities within its established home range, whereas dispersal refers to long

distance movements of an animal leaving one area of activity, apparently seeking a new home range.

Recording direct distance between telemetry relocations tends to under-estimate an animals actual travel distance, failing to account for meandering, or travels out and back from one site. Magoun (1985) reported that actual distances traveled were 33% greater than those calculated for wolverines she studied in arctic Alaska. Average daily distance traveled between relocations were 12.3 km for males and 4.2 km for females; one male on her study area was relocated 35.6 km from his location one day earlier. In the south-central Alaska study, Gardner (1985) reported the mean distance between relocations for both summer and winter was 13 km over an 8 - 10 day period. Males generally travelled twice as far as females. In the Yukon, daily movement averaged 1.5 km; one male kit traveled 17.3 km in one day (Banci 1987). Hornocker and Hash (1981) reported maximum movements over a three day period for males was 64 km and 38 km for females.

Unpursued male wolverines can travel 8.6 km/h; females 4.6 km/h (Magoun 1985). At these rates they certainly are capable of covering "...25 km in several hours " or "daily movement of 30-40 km from dens" (Hatler 1989), "33 km in a single night" (Wilson 1982), or "40-50 miles a day" (Rue 1981).

Simply because wolverines are capable of such dramatic movements, does not mean they necessarily make them at all times. Such movements are most likely in response to a shortage of food or the search for mates, and if these "resources" are available in one locale over a period of time, wolverines may become almost sedentary (Gardner 1985, Banci 1987).

Dispersal behavior

Studies invariably document some long range movements, usually dispersal by young males. Banci and Harestad (1990) documented a young

male that used a 400 km² area for three months, then apparently left for a month before returning. A marked female in Magoun's (1985) study was trapped 300 km south less than three months after she was originally tagged. Magoun (1985) also trapped a juvenile male 10 km south of his natal range a year later. Gardner (1985) and Gardner et al. (1986) reported a 2 year old male that was trapped 378 km to the east of the original capture site 20 months earlier.

Juveniles, usually males, apparently disperse to establish new territories. Gardner (1985) and Banci (1987) both ruled out food shortage as the reason for the dispersals they reported. Animals that fail to locate a home range probably become transients, moving to find food or to avoid confrontation with established wolverines. These dispersers, according to Hatler (1989), are probably responsible for reported range extensions (Newby and Wright 1955, Newby and McDougal 1964, Yocum 1973, and others). "From a management point of view, dispersal can be thought of as a 'natural transplant', and the existence of suitable refuges to disperse *from* is the mechanism most likely to prevent local extinctions and correct local declines" (Hatler 1989).

Seasonal elevation shifts

A few studies have documented seasonal elevation shifts. Gardner (1985) found distinct movement upward in spring to hunt emerging ground squirrels, and downward in fall and winter to ungulate winter ranges. Hornocker and Hash (1981) also found that both sexes moved to higher elevations during spring and summer, possibly responding to higher temperatures at lower elevations. Banci and Harestad (1990) speculated that "seasonal shifts by wolverines in Montana and Alaska appear to be responses to local environmental conditions and did not occur for most wolverines in the Kluane Game sanctuary during our study."

Territoriality

Wolverines are generally considered solitary animals. Males apparently associate with females only during the breeding season, and small family groups of a mother and her kits may be observed from late spring through the summer months (Hash 1987).

Rue (1981), citing work by Peter Krott, states that Eurasian wolverine males have territories of 500,000 acres, overlapping those of 3-4 females, that the boundaries of these territories are marked with urine, feces, and musk, and that they are defended. "Each wolverine honors the territory of another as a necessity to prevent overpopulation of a given area and the resultant food shortages." Rue (1981) also stated that North American wolverines do not usually have as large territories. Glacier National Park in Montana, encompassing about a million acres, is inhabited by about 30 wolverines, allowing each about 33,000 acres. "Calculating 8 males and 25 females and allowing for overlap, each male has about 125,000 acres, which seems about the right size." Rue (1981) concluded that a hunting wolverine may cover 40-50 miles in a day, and that " a male wolverine's territory is so large that it usually takes about 3 weeks for him to make a complete circle (depending) upon the availability of food and the weather" but cited no sources for this conclusion.

North American field studies of wolverines suggest that, with some exceptions, wolverines follow general Mustelid spacing patterns described by Powell (1979): studies of weasels, pine martens, and stoats have documented a basic mustelid spacing pattern of intrasexual territoriality, and: "...territorial behavior and food supply are believed to be the main factors affecting the maintenance and stability of this spacing pattern" (Hatler 1989). Powell (1979) wrote that "minks, black-footed ferrets, fishers, beech martens and wolverines (may) also exhibit this spacing pattern."

MacDonald (1983) speculated that among somewhat solitary predators, such as wolverines, bobcats, and weasels, female spatial organization may be determined by the distribution and availability of food, while male spatial organization is determined primarily by the distribution of females.

The field studies in Alaska and the Yukon seemed to suggest spatial relationships with little territorial overlap of like sexes , and overlap between sexes, but in all cases there were insufficient data to verify either case (Gardner 1985, Magoun 1985, Banci 1987). In contrast, Hornocker and Hash (1981) found considerable overlap between and within sexes in Montana, and no evidence of territorial defense; however, this population had a rapid turnover, and individuals had little time to establish territories.

Citing Hornocker et al. (1983) and Banci (1987), Hatler (1989) stated "(they) have all called attention to some practical difficulties and logical inconsistencies of a strict territorial system for this species. In particular, it is noted that for the large ranges required by the scavenging lifestyle, territorial maintenance would be very difficult and, given the unpredictability of food availability in some seasons, possibly unrewarding." Quoting Hornocker et al. (1983) Hatler (1989) noted that the wolverine has a "flexible" behavioral system that "... may be regarded as a positive adaptation to different and changing environments and is of value to the species survival," and concluded "that in any case, ... an individual's needs for food may supersede boundary considerations." Indeed, Banci (1985) and other authors have reported several wolverines congregating near an abundant food source at one time.

Marking behavior

The marking of trees, boulders, carrion, and food caches with urine, feces, and ventral scent gland secretions is well documented (Hornocker and Hash 1980, Koehler et al. 1980, Rue 1981, Wilson 1982,

Magoun 1985, Banci 1987, Hash 1987). Jackson (1961) stated that food caches are marked to signify ownership. Marking is often considered a territorial behavior (Rue 1982), and it is likely that Koehler et al.'s (1980) contention that marking maintains a temporal rather than areal spacing to avoid confrontation is correct. Hatler (1989) stated that "it seems clear that chemical signals cannot and do not prevent trespass." Whatever the reason, scent marking is a frequent and energy-consuming activity of the wolverine.

Temporal activity

Wilson (1982) stated that wolverine are primarily nocturnal, but may be active during the day as well. It appears that this statement may not be altogether accurate. Krott (1960) spent considerable time with free-ranging, semi-domesticated wolverines and concluded that the species was neither nocturnal nor diurnal, but displayed a more-or-less continuous sequence of activity and rest, alternating 3-4 hours regardless of day or night, though he noted that bad weather may induce longer periods of rest, and hunger longer periods of activity. Haglund (1966) claimed that the wolverine was the most likely large predator to be seen in daytime, calling its daily activity patterns "irregular."

Foraging behavior

In an interesting discussion on wolverine foraging behavior, Hatler (1989) cited work by biologists Krott (1960), Haglund (1966), Hornocker and Hash (1981), Magoun (1985), and others to suggest that wolverines do not hunt in the usual sense, but are simply "looking for something to eat." Tracks and direct observations by biologists and trappers, and many anecdotes of wolverine raids of food caches and traplines, suggest that the wolverine's most common winter foraging behavior is wandering about searching for caches made by itself, other wolverines, or other carnivores. "Further, and of particular relevance to management, that behavior is believed to make the wolverine particularly vulnerable to baited trap sets (Hash 1987)" (Hatler 1989).

POPULATION DYNAMICS

Density

Under the best of conditions, wolverine densities are low. Their occurrence and abundance is dependant upon a "diversity and abundance of food supplies" (Hash 1987). Van Zyll de Jong (1975) and Hornocker and Hash (1981) agreed that wolverine densities are greatest where there is a large and diverse ungulate population.

Hash (1987) stated that the greatest numbers of wolverines are found in the Yukon, the Northwest Territories, and Alaska, where remote areas support a variety of ungulate and small mammal populations and a "complex of efficient predators."

North American field studies confirm low wolverine densities even in the best habitats. Hornocker and Hash (1981) in western Montana identified one wolverine / 65 km^2 (40 mi^2) on their 1300 km^2 study area. Magoun (1985) estimated one wolverine/139 km^2 (54 mi^2) occupying the foothills and adjacent coastal plain of arctic Alaska; 1/48 km^2 (19 mi^2) for the foothills alone. Magoun (1985) believed these were underestimates, as they failed to account for transients.

In the Yukon, Banci and Harestad (1990) calculated one resident wolverine/ 177 km2 (68 mi^2), based on known wolverines in an area. If it is assumed that territories are exclusive by sex, Banci and Harestad (1990) calculated one resident wolverine / 93 km2 (36 mi^2). They pointed out that methods to calculate densities by various researchers have not been consistent (some include juveniles, some exclude transients, etc.) and that their reported density of 1/93 km2 included areas where wolverines were absent (due to poor habitat), thus overestimating actual densities.

Sex ratios

Sex ratios appear equal at birth (Wilson 1982, Hash 1987). In exploited populations females tend to outnumber males, as the males are apparently more vulnerable to trapping, as they travel more, are often the (frequently half-starved) transients. Magoun (1985) noted that since there are fewer male home ranges available, since they are so much larger than female home ranges, there will be more males in the transient category. In Montana, trapped males outnumber females 2 to one (Hash 1987).

Cycles

One author maintained wolverines cycle in response to hare abundance as do lynx (Bulmer 1974, 1975), but others found no evidence of consistent cycling (Cowan 1938, Holbrow 1976). Hatler (1989) concluded: "It is evident that population fluctuations occur, but apparently not in any regular, predictable pattern." No doubt wolverine populations do fluctuate with the abundance of food availability, and anything that effects animal abundance over a widespread area would effect wolverine abundance over a period of time.

FOOD HABITS

Nutrition

Wolverine metabolism, measured under laboratory conditions, was found by Iverson (1972) to be about 20% higher than expected from body size. Hatler (1989) surmised that the nickname "glutton", suggesting a voracious appetite, came about from observations of encounters with very hungry individuals, whereas captive or well fed animals display no particular tendency to over-eat. He suggested that occasional intense hunger is a probable fact of life for any animal relying largely on climatic factors and other carnivores for its next meal.

Two of the four major field studies of wolverines in North America prior to 1990 had marked animals that were suspected to have died of starvation (Hornocker and Hash 1981, Banci 1987) and in a third, Magoun (1985) thought inadequate nutrition resulted in widespread reproductive failure during her study in Alaska. Banci (1987) found 23% of the wolverines she examined had empty stomachs.

Food

The wolverine "will eat anything edible (it) can catch , find, or steal" (Rue 1981). In all North American field studies carrion has played a significant portion of the diet, particularly in late winter and spring (Hornocker and Hash 1981, Gardner 1985, Banci 1987, Magoun 1987a). Other foods that occurred in high percentages, especially during the summer and fall, were ground squirrels, snowshoe hares, mice and voles, and blueberries. Banci (1987) warned against identifying one prey group as most important to wolverines, emphasizing the uncertainty and unpredictability of food sources. Following her advice, Hatler (1989) listed all foods reported in the literature. This list includes 7 ungulates, 8 rodent genera, 13 other mammals, 6 kinds of birds, plus eggs, plus fish, insects, berries, and garbage, seeming to confirm Rue's statement above.

Most ungulates are obtained through scavenging carrion, though wolverines have been observed successfully attacking large mammals in deep snow (Burkholder 1962, Wilson 1982), including caribou (Burkholder 1962, Magoun 1985), and reindeer (Haglund 1966). Snowshoe hares ranked second in occurrence in the diet of wolverines in the Yukon and Alaska. Hatler (1989) speculated that, since snow-tracking observation by Haglund (1966), Hornocker and Hash (1981), and Gardner (1985) showed no evidence of wolverines hunting by stealth or strategy, hares were probably killed by other predators and scavenged by wolverines. Wolverines can and do hunt and capture smaller prey, primarily marmots, ground squirrels, mice and voles. Rodents also become wolverine food in the winter as they are dug out of caches and eaten (Gardner 1985).

CURRENT STATUS

Wolverine populations in Alaska and western Canada are trapped and hunted in most areas, but populations appear to be fairly stable. The situation in the Lower 48 seems less clear. As of the early 1990's, Montana still classified the wolverine as a furbearer (and has since 1976) with an annual trapping season. Harvests have fluctuated for decades, depending as much upon fur prices and severity of winter as on wolverine populations. Annual harvests in the 1960's and 1970's were generally between 10 and 15, though 58 were taken in 1976. The high for the past 30 years. In the 1984-1985 season, 25 were harvested. The harvest was 11 in 1989, 7 in 1990, and 5 in 1991 (Tom Hinz, MT Fish Wildlife and Parks, pers, Comm, March 12, 1992).

Nevada considers the wolverine extinct, and unprotected. It is classified as a furbearer in Montana, a protected non-game animal in Idaho and Washington, threatened in California and Oregon, and endangered in Colorado. Federally, it is classified by the Fish and Wildlife Service as a Category 2 species (C2 = Taxa for which information now in possession of the Service indicates that proposing to list as endangered is possibly appropriate, but for which conclusive data on biological vulnerability and threat are not currently available), and as sensitive in Regions One, Four and Six of the USFS. The Forest Service defines "sensitive" as a species for which population viability is a concern as evidenced by significant current or predicted downward trends in population numbers or density, or habitat capability (Table 1).

Idaho began a successful effort to document wolverine in the state in 1989 (Bachman et al. 1990). California has also begun such an effort, but have yet to document wolverines (Kucera and Barrett 1991). Colorado nongame specialists have attempted to locate wolverine and lynx since the late 1970's (Halfpenny et al. 1979, Nead et al. 1984). Utah has finished a review of sightings and may be taking steps soon to document wolverines in the Uinta Mountains (McKay 1991).

Table 1. Status of the wolverine by agency.

U.S. Forest Service	
Region 1	S
Region 4	S
Region 5	S*
Region 6	S
U.S. Fish and Wildlife Service	Category 2
Bureau of Land Management	S
State Agencies	
California	T
Colorado	E
Idaho	NG
Montana	FB
Oregon	T
Utah	-
Washington	P
Wyoming	-

S = Sensitive
T = Threatened
NG= Nongame species
P = Protected species
FB= Furbearer
E = Endangered

S* = Proposed as sensitive

MANAGEMENT

Population management

Wolverines are primarily considered a fur resource in Alaska and Canada, though their pelts are not considered particularly valuable (Hatler 1989). Currently, Montana is the only state south of the Canadian border that allows the taking of wolverine as a furbearer.

Where wolverines are harvested, the recommendations of Hatler (1989) for British Columbia may be appropriate. He recommended the following management activities and options:

1) Where trapping pressure may be too heavy, shortening the season at the end will provide protection for resident males and productive females before they reach maximum vulnerability. Hash, 1987) recommended closures after January to protect females with kits;

2) Quotas per trapper will probably not reduce the harvest of wolverines as most trappers rarely take more than one or two. Regional quotas, that allow an area to be closed to wolverine trapping when the quota is reached (requiring mandatory reporting of the taking of a wolverine within a specified time period, such as 48 hours), can allow for a limited harvest.

3) Hornocker and Hash (1981) and Hash (1987) suggested the curtailment of the use of baited sets for all species in areas where wolverine expansion is desired. Hatler (1989) noted that this regulation would be difficult to enforce, and also noted that the use of baited sets would most likely produce compensatory harvests. He also pointed out that the often used regulation of requiring the use of killer type traps, such as "conibears," for humane reasons, is ironic in that wolverines are notorious for escaping from leg-hold traps to live another day, and thus become an "educated" and more secure segment of the population.

4) As the maintenance of refugia appears to be so important to maintaining secure wolverine populations, Hatler (1989) suggested that when new areas are opened up for development, that trappers resist exploiting all areas that become accessible.

Given the relatively low densities of wolverines in the United States south of the Canadian border, continued or expanding demands for timber, mining, home development, and recreation, the pressures on the remaining wolverines and their habitat will continue to grow. To maintain viable wolverine populations in these areas, it seems difficult to justify any legal wolverine harvest. The few wolverines taken south of Canada certainly provide little recreation or fur income. In areas of potential wolverine use, or in areas of potential wolverine expansion, trappers and trapper associations can take an active role in learning ways to minimize the accidental take of wolverines, how to safely release those accidently caught, and how to turn in any accidently killed without penalty.

Wherever the species is harvested, Hash (1987) recommended mandatory registration of the kill to provide information on harvest numbers and distribution. The collection of skulls, recommended by Magoun (1985), can provide sex and age data with little trouble to the hunter or trapper.

Habitat management

In general, wolverines need large undisturbed areas with an abundance and variety of small and large mammals (Van Zyll de Jong 1975, Kelsall 1981). In the southern portions of their range, including all of their range in the "lower 48", they use mountainous, coniferous habitats (Hash 1987). They appear capable of re-populating areas of suitable habitat as long as they have refugia to re-populate from, such as large wilderness areas (Newby and Wright 1955, Allen 1987, Hash 1987). They avoid clear-cuts (Hornocker and Hash 1981).

In addition to the maintenance of wilderness areas for refugia, Allen (1987) recommended providing a variety of successional stages, maintaining or encouraging a cover type mosaic through cutting or burning, and maintaining travel corridors between extensively managed areas and wilderness.

If the goal of a wolverine management plan is to optimize population size, Wilson (1982) suggested "it is possible the best way to manage this species is to do nothing. Wolverines would probably flourish if sufficiently large tracts of proper habitat were set aside and protected." Recognizing the difficulty inherent in this recommendation, he continued: "it is not always possible to provide totally protected refuges in areas where it may be possible to maintain wolverine populations. Protection from human predation should be provided in all areas of the contiguous United States."

Hatler (1989) stated "habitat management for wolverines is not simple, requiring attention to the total ecosystem perhaps more than for any other species." He continued: "the reduction of wilderness "refugia" through access and alienation for timber and mineral extraction may be the greatest threat to local population viability (and practices that) reduce biological diversity are all potentially negative for the species. In effect, successful management of wolverines requires a successful integrated management system for all the other wildlife species for which it depends."

Wolverines are quite capable of living in a variety of habitats as long as enough food and security is available. They are usually associated with wilderness chiefly because they are so vulnerable to the activities of humans (V. Banci, pers. comm., 1992). Therefore, specific habitat management guidelines must include some means of providing security and protection from man, and they must provide for an adequate year-around food supply. Guidelines established for the grizzly bear or the lynx will have applicability to the wolverine. The key to management is:

1) the less development, the better. Roads, if necessary, should be one way (not loops), as primitive as possible, and permanently closed after mineral or timber entry is completed.

2) timber harvest should be accomplished in a manner that will provide the greatest biological diversity over the long term. Cuts should be relatively small, not adjacent to large openings, leave some down material and some understory for small birds and mammals, and provide for travel corridors between secure cover areas.

3) carcasses of big game are an important component of wolverine late-winter diet, especially in areas with long and intense winters (most of wolverine range). Activities that encourage maintain ungulates and their winter ranges will benefit wolverines.

TECHNIQUES

Age determination

Development of life histories for any animal requires accurate age classification of study specimens. The most common technique used to age mammals for the past twenty years has been cementum tooth analysis. This assumes that the number of cementum bands deposited have a direct correlation to the age of the animal. The age determination of wolverines using this method is difficult (Banci 1982b), but it has been the primary method used by all North American field studies to date.

Rausch and Pearson (1972) and Banci (1982b) looked at alternative methods of aging wolverine. Both reported that skull measurements can be used reliably to distinguish young-of-the-year from adults. Banci (1982b) found some utility in using the length of sagittal crest in males, and the degree of closure of internasal and zygomatic sutures for both sexes to determine age.

Cementum analysis is probably still the best technique, though it

has inherent problems. Though Banci (1987) suggested using incisors or premolars for analysis, Gary Matson of Missoula, a professional histologist, has found best results using canines from wolverines (Matson, pers. comm., Mar. 12, 1992). For wolverines captured live, to be released, a premolar will suffice for age determination. As Banci (1987) pointed out, "differing methodology, even within the same technique, can bias results and make comparisons between studies untenable." Consistent use of a professional laboratory by researchers would do much to reduce this bias.

Immobilization techniques

Wolverines were captured in live traps by Hash and Hornocker (1980) and immobilized using ketamine hydrochloride (Ketalar 100mg/ml) administered by intramuscular injection into the hip area. Dosages recommended range from 17.22 to 25.52 mg/kg body weight. Males required a higher dosage per kg body weight. Mean time to immobilization was 3.83 minutes, immobilization lasted an average of 44.28 minutes (range= 18-68 min.), and recovery took an average of 46.28 min. (range= 15-75 min.). No wolverines died from this treatment, and there were no noticeable ill effects. They also administered 2 ml bicillin to prevent infection and recommended use of a muscle relaxant such as xylazine hydrochloride to reduce muscle rigidity, a side-effect of ketamine.

Banci and Harestad (1990) reported using a mixture of ketamine hydrochloride and xylazine hydrochloride (Rompun). Banci (Unpub. rep.) stated that "the attractiveness of this combination is that it is fast acting, relatively short in duration, has a wide safety margin for both animal and human and is relatively cheap." They gave no dosage information.

Survey techniques

Because wolverines occur in such low densities they are difficult to survey. McKay (1991) summarized methods that have been used to survey for wolverines. Some of these methods are used to verify wolverine presence, while others have been used to monitor known populations. She listed:

1. Literature review of historic occurrences (Durrant 1952, Hoak et al. 1982, Groves 1987).

2. Mail questionnaire (Hoak et al. 1982, Groves 1988).

3. Rare mammal survey using "Wanted posters" (Groves 1988).

4. Bait and/or scent stations with hair traps (Groves and Gadwa 1989, Bachman et al. 1990).

5. Bait and/or scent stations with infra-red cameras (Bachman et al. 1990, Kucera and Barrett 1991).

6. Scent stations in summer for tracks (Winn 1976, Roughton and Sweeny 1982).

7. Radio telemetry (Hornocker and Hash 1981, Hash 1987).

8. Live traps (Hornocker and Hash 1981).

9. Aerial surveys (Hash 1987).

10. Winter track surveys (Austin 1990, Bachman et al. 1990, Koehler 1990).

Each of these techniques has inherent advantages and

disadvantages, and some are more appropriate than others, depending on data required, and finances available. The Monitoring Committee of the Interagency Lynx-Wolverine-Fisher Working Group has been developing a dichotomous key to allow a user to select the appropriate method for surveying or monitoring wolverines, depending on the management objectives. It is the desire of the Working Group to promote standardized techniques, and to see that they are used most effectively and efficiently.

The Monitoring Committee suggested that the selection of a detection device to be used in a monitoring program be: 1) affordable, 2) able to verify with evidence, 3) easy to transport and establish, 4) standardized, and 5) simple to use by all cooperators.

Different levels of monitoring intensity were identified. These are:

I	Presence or absence
II	Distribution
III	Population trend
IV	Population size
V	Population composition

The Committee developed a list of monitoring techniques and listed their advantages and disadvantages for Level I monitoring for wolverines (Table 2). It is the intent of the Committee to complete an analysis of these techniques and to analyze their costs for Levels I through IV for lynx, wolverine, and fisher, and to produce a manual outlining their recommendations, as well as producing training materials and workshops to disseminate this information.

Table 2. Monitoring techniques.

IV. Level 1 - Wolverine.

Listed below are the techniques considered, in order of increasing dependence on sophisticated technology, for wolverines at Level 1.

Technique	Advantages	Disadvantages	Costs
1. *Incidental sightings* of individuals and their sign.	Low cost; Many observers; Large area covered; Good PR; Educational; Used at any season; Can ID areas for future work.	Sightings need verification; No control over effort; Limited to visitor use areas; Presence only-limited confidence in absence.	Posters; Brochures; Data entry; Training; Verification.
2. *Surveys*:			
a. *Snow track counts* (trained personnel who return with physical evidence; photo, measurements)	Reliable data on multiple species; Large area covered; Simple-few instruments/hardware; Flexibility of scheduling; Good data on absence.	Need adequate and proper snow cover; Labor intensive.	Transportation; Survival gear; personnel training; Additional gear- cameras tape, film, etc. Costs depend on mode of travel - foot, snowmobile, aircraft.
b. *Track-plate counts* (sooted and partially covered with contact paper; baited and enclosed in a "cubby")	Positive ID; Good pad print provides physical evidence from which accurate measurements can be collected; Bait and lure increases detections; Can be used all seasons and when access is best; Easy to schedule; Data on a number of species; Immediate ID not necessary.	No gait pattern; Limited to certain species; Bait/lure can alter behavior; repeat visits by personnel are necessary; More gear needed to transport and set-up; Non-target species can inactivate the station.	More than snow-tracks...(?)
c. *Hair snares* (baited cylinders of wire)	Provides physical evidence; Used during all seasons and by many species; Bait/lure increases detections; Technicians need not be too skilled; Immediate ID not necessary; Potential for genetic ID to species.	ID based on structural characteristics is difficult; Hair is infrequently snared; Bulky; Negative PR.	Similar to track-plate....
d. *Cameras*			
1. *"Low -tech"*; (110 print film; manual trigger)	Inexpensive; Can be used for other studies; Physical evidence and positive ID; Bait/lure increases detection; Used all seasons; Used when access is best; Ease of scheduling; May recognize individuals.	Vulnerable to weather; Relatively high failure rate; Small negative; Trigger requires that subject must pull bait; Non-target species inactivate the station; Limited to 1 photo per visit; Repeat visits necessary to service; Experience technicians necessary; No time/date on film.	Similar to track-plate...

PART II WOLVERINE LITERATURE

There have been four comprehensive wolverine bibliographies published in the past: Dagg and Campbell (1974a) included 287 references with keywords, Banci (1982a) contained 607 titles, Halfpenny et al. (undated) listed 626 references in nine different subjects, and Hatler (1989) included 180 annotated titles. Hatler is perhaps the most useful, containing most recent citations, including most of the pertinent papers with information on life history and management of the species, and an excellent subject index, though both the Banci (1982a) and Halfpenny et al. (undated) bibliographies contain a very diverse and comprehensive collection of references on the wolverine. A fifth bibliography, containing 52 annotated citations, is contained in McKay (1991).

Any comprehensive attempt to review and comment on the literature has to have some boundaries, and often these are subjective. Dagg and Campbell (1974a), Banci (1982a), and Halfpenny et al. (undated) included almost everything ever written on the wolverine. Hatler (1989) focused on North American literature, especially that relevant to life history and management, as well as everything published on the wolverine in British Columbia. McKay (1991) included some of the classic literature and everything pertaining to wolverines in Utah that she could locate.

This work focuses on management of the wolverine in the contiguous United States, primarily in the mountainous west. The bibliographic sections of this document are composed of four parts:

I. Bibliography

This section includes papers that pertain to the biology and management of the wolverine in the western United States. It has but one specific reference to wolverine

parasites and diseases; the reader may refer to this paper, or other "general" references for further information on this topic. Because the majority of extensive field work has been done in Canada and Alaska, literature from these areas is referenced when it provided valuable information on the life history or management of the species. Some of the classic literature from Eurasia has also been referenced, especially if it contains new or more in-depth information than that available in North America, was generally obtainable in the United States or Canada, and had at least an English summary.

Abbreviated keywords follow each citation in **bold**, indicating some of the topics discussed in that paper.

KEYWORDS

behav- behavior, foraging behavior
biblio- bibliography
dens- density
distrib- distribution
food- food habits
habitat- habitat
hab mgt- habitat management
harv- harvest
health- diseases and parasites
hist distrib- historical distribution
home rng- home range
immob tech- immobilization techniques
lif hist- life history
lit rev- literature review
pop mgt- population management
status- status

surv tech- survey techniques

taxon- taxonomy

terr- territory

tech- techniques (age/sex determination,

II. Subject Index

An index of topics referenced by keyword to each bibliographic citation is included here.

III. Annotated Bibliography

Papers that I judged were fairly important contributions to the literature, including classic field studies, in-depth literature reviews, and studies directly pertaining to the management of wolverines in the western United States were included in this section. As Hatler (1989) and McKay (1991) had previously annotated much of this literature, I have used their annotations where possible.

Hatler (1989) listed the citation, followed by three alphabetical codes, and comments. The codes he used are: A) a significance rating of 0-3, with 0 rated as insignificant and 3 as very significant; B) geographic area considered in the paper; and C) a short description of the contents of the paper. All annotations from Hatler (1989) are noted with an asteric (*). Annotations from McKay (1991) are marked with two asterics (**) before the citation.

PART III. SELECTED REPRINTS

Copies of the papers I judged most significant to the biology and management of the wolverine are included in their entirety in this section.

WOLVERINE (*Gulo gulo*) BIBLIOGRAPHY

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terr, dens, behav, immob tech

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ANNOTATED BIBLIOGRAPHY

Annotated bibliographies of a number of important papers on wolverine biology and management are included here. David Hatler (Hatler 1988) and Robin McKay (McKay 1991) have given their kind permission to select and copy from the excellent annotated bibliographies that they have compiled. Hatler's annotations are marked with (*) and McKay's with (**).

Hatler (1988) listed the citation, followed by three alphabetical codes, and comments. The codes he used are: A) a significance rating of 0-3, with 0 rated as insignificant and 3 as very significant; B) geographic area considered in the paper; and C) a short description of the contents of the paper.

Austin, D.A. 1990. Summary report, winter snow track count surveys, timber sale project opportunity areas. Mt. Hood National Forest. Columbia Gorge and ZigZag Ranger Districts. **

Animal track surveys occurred on established roads using snowmobiles, snowshoes, and cross country skis. The surveys occurred as soon after fresh snow fall as possible. Tracks were photographed for verification. Aerial photos were used to pinpoint track locations.

Bachman, D., G. Gadwa and C. Groves. 1990. A winter survey for wolverines (Gulo gulo) on the Sawtooth and Challis National Forests, Idaho. Idaho Fish and Game, Boise. 29 pp. **

A full description of the methods and results for a January to April 1990 winter survey for wolverines, primarily on the Sawtooth National Forest and to a lesser extent the Challis National Forest is presented in this paper. Researchers utilized snowmobiles, skis, and snowshoes to locate wolverine sign. Areas exhibiting past wolverine use were monitored by bait and scent stations. Hair traps and remote infra-red sensitive cameras were used to monitor wolverine presence at bait and scent stations. Hair traps did not collect any wolverine fur, suggesting to researchers that this method may be inefficient for locating wolverines.

During this study, 14 track sightings were "confirmed" and 3 were designated as "probable". Habitat use inferred from these data suggest that wolverines appeared to mostly utilize mixed conifer habitat with preference for spruce\fir stands along stream bottoms. Of secondary use were areas of mature lodgepole pines. It appeared to researchers that wolverines use the same winter areas from year to year.

Cameras collected pictures of wolverines and a variety of other animals at the bait stations. Researchers suggest that the use of cameras is good for monitoring wolverines.

* Bailey, T.N. 1981. Factors influencing furbearer populations and harvest on the Kenai National Moose Range, Alaska. Pages 249-272 *in* J.A. Chapman and D. Pursley (eds). Worldwide furbearer conference proceedings, Aug. 3-11, 1980, Frostburg, Maryland.

A) 1; B) Alaska; C) Review of furbearer and harvest data on the refuge.
Population Dynamics - poptrend.
Species Management - harvest.
Habitat Management - fire.
Comments - It is speculated that "since prime habitat of wolverines on the refuge appears to be along the more rugged mountainous forest edges and alpine areas, fires probably have not significantly influenced wolverine habitat"; initial impact on prey species might be detrimental, but wildfire effects on food supply would probably be beneficial in the long term.

* Ballard, W.B., A.W. Franzmann, and C.L. Gardner. 1982. Comparison and assessment of drugs used to immobilize Alaskan gray wolves (*Canis lupus*) and wolverines (*Gulo gulo*) from a helicopter. J. Wildl. Dis. 18:339-342.

A) 2; B) Alaska; C) Monitoring of results during field use.
Species Management - gen/tech.
Comments - Etorphine is favored for use on these two species because it enables quick recovery and therefore does not expose animals to prolonged exposure to extreme temperatures or accidents; a dosage of 0.7 mg etorphine mixed with 50 mg of xylazine is recommended for aerial darting of wolverines weighing 10.5 - 17.7 kg.

* Banci, V.A. 1982a. A bibliography on the wolverine *Gulo gulo*. Research, Ministries of Environment and Forests. IWIFR-9. Victoria. 53pp.

A) 2; B) General; C) Literature search and compilation of references.
Other Topics - bibliography.
Comments - This is the most complete of the wolverine bibliographies in terms of number of titles (607), although the treatment of the species in a large proportion of that total is little more than a mention of the name; further, it consists only of a simple list, without annotations or topic headings, making it less useful than it otherwise might be.

* Banci, V.A. 1982b. The wolverine in British Columbia: distribution, methods of determining age and status of *Gulo gulo vancouverensis*. Research, Ministries of Environment and Forests. IWIFR-15. Victoria. 90pp.

A) 2; B) British Columbia; C) Literature review and examination of museum specimens.
Description - taxonomy, distribution.
Species Management - age/tech.
Comments - A comparison of skull features and dimensions leads to the conclusion that the Vancouver Island wolverine is not sufficiently different to warrant a separate subspecies status; age determination in wolverines is difficult because the species grows and matures quickly-- there were no significant correlations with age among several combinations of cranial and dental measurements; an "enamel line" technique was evaluated and found of little use for the species; annuli are present in dental cementum, but teeth are difficult to prepare, resulting sections are difficult to read, and there is little known age material to correlate annuli numbers and age; further, wolverines may show more variable cementum deposition patterns than most species because they experience less pronounced seasonal nutritional differences (food is often most available to them in winter) and/or because there may be more variation in nutritional patterns between years; for those reasons, and because juveniles and subadults are difficult to separate by the method in any event, cementum annuli analysis may not be appropriate for wolverine--preliminary results with a technique involving measurement of the canine pulp cavity have been promising; a provincial distribution map, compiled from literature records, anecdotal accounts, and harvest records show that the species occurs throughout B.C., but probably most significantly in the northern half, although observations and records anywhere along the coast are rare; the need for information on habitat requirements and population characteristics in the province is emphasized.

* Banci, V.A. 1987. Ecology and behavior of wolverine in Yukon. Unpubl. M.Sc. Thesis, Univ. British Columbia, Vancouver. 178pp.

A) 3; B) Yukon Territory; C) Field studies with telemetry and laboratory study of 461 trapped specimens, 1982-1985.
Description - features, distribution.
Habitat Characteristics - study area, cover, climate.
Life History - food, hmrange, movements, dispersal, socbehav, behavior, health.
Population Dynamics - natality, mortality, poptrend, popcomp, popreg.
Species Management - age/tech, kill/tech, repro, harvest, harv/strategy, interactions.
Comments - This study represents the most thorough and wide-ranging field study of the species that has been undertaken in Canada, and since there has as yet been no formal publication of results in easily obtainable sources, detailed coverage is provided here; **REPRODUCTION** - among 180 usable female samples, 109 (61%) were in the first two age classes, with all of 82 kits (age 0+) and 25 of 27 subadults (1+) in the "non-reproductive" category; for the 71 older animals, those found to be in the reproductive (pregnant or post-partum) group included 16 of 30 in age 2+, 12 of 13 in each of 3+ and 4+, 6 of 7 in age 5+, and only 3 of 8 in a combined 6+ - 11+ group; overall, owing partly to the young age distribution of the sample, only 53 of 180 females in the sample (29.4%) were in the reproductive class; the mean *in utero* litter size was 3.2, and there was evidence for litter size increasing with age of female, ranging from 2.8 to 3.4 in ages 2+ to 5+; it is emphasized that the laboratory results, though indicating low productivity, probably are nevertheless optimistic because they fail to account for intra-uterine and pre-weaning losses; implantation occurred as early as November and some births as late as March, but there was some evidence that most parturition may be in February; males were sexually mature at 2+ years, and showed some evidence of increased breeding condition by late winter (March); **AGE DETERMINATION** is a problem for this species--though not considered ideal, dental cementum analysis using upper premolars was used in this study; **FEATURES (SIZE)** - adult males were heavier than younger animals, but body measurements did not differ--estimated whole weights for kits, subadults, and adults, respectively, were 11.5 kg (n=59), 11.9 kg (n=44), and 12.8 kg (n=111); comparable weights for females were 8.3 kg (n=60), 7.9 kg (n=30), and 8.7 kg (n=82)--the lower figures for subadult females was possibly due to weight loss during their initial period of independence (a year later than for males); the largest estimated weights were 14.4 kg (female) and 21.3 kg (male); whole weights of live-trapped males varied from 10.2 kg for a kit to 15.0 kg for an adult aged 10+, and averaged 13.0 (n=5)--comparable figures for females were 6.6 and 7.8 kg for two kits, up to 11.0 kg for an adult, with a mean of 8.7 kg (n=5); **CONDITION** - a kidney fat index and a visual estimate of total body fat were both considered inadequate for measuring condition, although there was some evidence that females were in low in body fat more often than males; **FOOD HABITS** - detailed comparisons of stomach contents for quick-killed and restrained animals indicated that consumption of trap bait was rare and unlikely to bias food habits results; based on 411 stomach, 95 (23.1%) were empty-- suggesting that food was generally difficult to obtain; frequency of occurrence and percent dry weight of major prey items in the remaining 316

stomachs was snowshoe hare (18.5, 6.7), porcupine (10.9, 0.8), moose (9.7, 12.5), caribou (5.4, 8.0), red squirrel (4.4, 0.7), and ground squirrel (2.4, 0.9); flesh, fat, and bone not identified to specific groups, but believed mostly from wild ungulates, had a combined frequency of 32.9% and a percent dry weight occurrence of 31.0--that category combined with the identified ungulate remains demonstrates its major importance in the diet (believed mostly scavenged); other ungulates identified (besides moose and caribou) were elk, mule deer, thinhorn sheep, and mountain goat, all at occurrences and dry weight percentages of 2% or less; other prey remains, all at low incidence, were shrew, pika, chipmunk, flying squirrel, marmot, beaver, at least 4 species of microtines, traces of marten, mink, weasel, coyote, wolf, lynx, unident. fish, and birds from at least 4 families; the greatest diet variability in the sample period was in November, when snow cover is usually least; the hibernators among the small mammal prey were believed taken from caches; small mammals were rarely found in the same stomachs with ungulates, suggesting that they were hunted when larger items were not available; snowshoe hare occurrence (the most frequent identified item) was despite the fact that the study commenced during the year of the species' cyclic decline; other evidence of food use included observations of wolverines carrying or chasing ground squirrels, tracks indicating hunting of ptarmigan, use of spawned salmon frozen into river ice, and use of garbage at a camp; in addition, 5 of 12 winter scats contained kinnikinnick berries; **HOME RANGE** - 10 wolverines were radio-collared, but only 5 (3 adult females, 1 adult male, and 1 subadult male) were monitored significantly; all 3 adult females made long distance "excursions" in summer, but without those (whose purpose was not determined), summer and winter ranges were similar in size; only 1 of the 3 females produced young, and her annual home range (139 km^2) was half that of the two without kits (202 and 343 km^2); the adult male's range (238 km^2) was only slightly larger than the average for the females and was much smaller than that of the juvenile male (526 km^2), whose movements suggested dispersal; animals sometimes remained in relatively small areas for long periods, presumably because a large food supply (perhaps one or more ungulate carcasses) was available in that area--range size appears generally related to food availability for both sexes, although access to females may also be a factor for males; **MOVEMENTS** - daily movements were generally small, averaging less than 1.5 km/day for most individuals--the longest single daily movement recorded was 17.3 km, by a male kit; **MORTALITIES** among collared animals included a) a subadult male and an old (age 10+) male, both trapped (outside the study area?), b) a male kit apparently killed by wolves, c) an old adult female that first sustained an injury (believed by a wolf), and after being recaptured 3 times in the month following, died in captivity--autopsy showed "parasitic pneumonia" and a kidney disease, d) a female kit believed to have starved, and e) another female kit whose cause of death was "...suspected to be starvation and/or injury"; the energetic demands of producing and feeding young are emphasized as a major potential factor in the condition and survival of females--the one that eventually died in captivity was suspected to have been "weakened" initially in that way; reference is also made to an apparent wolf kill of an uncollared adult male; **HABITAT** use did not differ from availability for females, either generally or seasonally; both collared males used subalpine conifer habitat more in winter and alpine talus less in summer than expected based on availability; there were individual variations, but when data were combined by sex, there were no significant patterns of use of different aspects, elevations, or percent forest cover types; **TERRITORIALITY** - little information on range overlap between and among sexes was obtained although scent marking, especially by residents, was recorded;

HARVEST - in regard to harvest patterns, it is acknowledged that climate and economic factors, which may vary from year to year, influence trapper activity; the sex ratio of the harvest varied from 1:1 significantly in only 1 of the 3 study years, but was significant at 1.3:1 in favor of males for the overall sample 258:204; age ratios were not different within sexes or among years, the total harvest comprising 213 juveniles and 200 adults (2+ and older); male kits showed the earliest vulnerability, as the class caught most often in November-January in all years (peak in January); subadult males had a harvest peak in February, possibly their dispersal time; subadults were the smallest harvest class; female kits appear to establish ranges in their natal areas and were apparently not particularly vulnerable until later in the winter (a pattern similar to that for adult males); adult female harvest peaked in February, possibly as they became more mobile and vulnerable to meet the nutritional requirements for parturition and lactation; NUMBERS - based on population indices developed for trapped ecoregions, and an estimated density of 1 resident per 177 km^2, the total Yukon wolverine population was estimated at about 4380 animals; GENERAL CONCLUSIONS - availability of food is considered a major factor mediating range size, movements, possibly timing of parturition, reproductive success, and survival of young--vagaries of climate and its seasonal effect on large ungulates is one of several complicating factors; bad winters for ungulates are probably good for wolverines; "As food resources are not consistent among areas nor over time, patterns of habitat use are expected to vary seasonally and locally."; no single habitat type can be identified as important for the species, but large areas providing a diversity of habitats are believed to be required; HARVEST STRATEGY AND RECOMMENDATIONS - differential vulnerability of sex and age classes may offer some opportunity for harvest control, although the actual vulnerability pattern of females is still unclear; it is suggested that during winters when availability of food is low, reproduction may be affected and harvest pressure should be reduced; finally, it is recommended that the species status as "big game" should be changed and hunting (which accounts for about 10% of the annual harvest) stopped, since it probably does not act on normal vulnerability patterns, and usually takes animals when pelts are inferior.

Banci, V. and A.S. Harestad. 1990. Home range and habitat use of wolverines *Gulo gulo* in Yukon, Canada. Holarctic Ecol. 13:195-200.

Life History
Yukon

ABSTRACT
Home ranges and habitat use are described for three adult female, one adult male, and one subadult male wolverines in the Kluane Game Sanctuary, Yukon. When long distance excursions are not included, home ranges of wolverines in the Kluane Game Sanctuary were between 76 and 269 km^2 for males. Habitat use of females was similar to habitat availability. Males used subalpine coniferous habitats more frequently than other habitat types during winter. Although individual variation in the use of forest cover types, aspects, slopes, and elevations was apparent, seasonal use did not differ from availability for each sex. Within the 1590 km2 study area, three adult males and six adult females were present, corresponding to a density of one resident wolverine /177 km^2.

Barker, M.S. Jr., and T.L. Best. 1976. The wolverine (Gulo
** luscus) in Nevada. Southwestern Naturalist 21:133.

A wolverine skull was found in a cave located 11.3 kilometers south of Baker, White Pine county.

Barnes, C.T. 1927. Utah mammals. Bulletin University of Utah
** 17(12):43.

This book is commonly referenced for historical information regarding the mammals of Utah. Records of wolverine specimens or sightings are documented in a chapter dedicated to this species and are summarized as follows: (1) In 1893, Brigham Spencer of Moab, Utah, said he saw 2 adult and 2 young wolverines on Boulder Mountain in Garfield county. Brigham supposedly collected one of these animals. The last time he saw them was in 1897. (2) Theodore Suholser of Logan, Utah, said several wolverines had been trapped near Logan and are some still remain in the high timber of the Uinta Mountains. (3) Mr. Frank Sargent has occasionally seen one in the Mt. Baldy region of Piute county.

Burkholder, B.L. 1962. Observations concerning wolverine. Journal
** of Mammalogy 43:263-264.

During January 1953, while studying wolves in Alaska, Burkholder observed from an airplane an average sized wolverine attacking a male, antlerless caribou (Rangifer taranadus), also of average size, on a frozen river. The wolverine was observed making short dashing movements toward the caribou. The wolverine tried to attach itself to the head several times, but was thrown off. The wolverine then out-maneuvered the caribou, jumped up on its back an attached itself just behind the withers, and the caribou finally collapsed. After returning two days later they found the caribou dead and partially consumed by the wolverine.

Another interesting observation by Burkholder was that of a wolverine carcass found near a dead caribou (probably abandoned during hunting season). The wolverine had dug through snow to uncover the caribou. Judging from tracks in the snow, the wolverine was pursued and killed, but not consumed by a pack of wolves.

Coues, E. 1877. Furbearing animals: a monograph of North American mustelidae. United States Geological Survey of Territories
** (Hayden) Miscellaneous Publication Number 8. Government Printing Office. Washington D.C. 348pp.

This book provides a systematic history of North American mammals. This volume deals solely with members of the mustelidae family. Aspects discussed include the following: generic characteristics, synonymy, habitat, specific characters, description of external characters, measurements, anal glands, description of the skull and teeth, skull measurements, nomenclature, general history, geographical distribution, habits, and the distribution in the old world.

Wolverine specimens documented include: Mr. C.H. Merriam collected a specimen from along the Yellowstone River, Wyoming during August 1872. Professor S.F. Baird notes the specimen from Captain Stansbury's expedition, taken from the Great Salt Lake. J.A. Allen saw the skin of a wolverine taken in the vicinity of Montgomery Colorado, and suggested that the animal was a common occurrence. E. Coues also saw a mounted specimen belonging to Mrs. M.A. Maxwell, near Boulder Colorado.

Also discussed in this historical document is the fact that wolverines were an annoyance to trappers, in that wolverines raided marten trap lines. After eating their fill, the wolverines were observed caching the bait remaining on the trap line. They were also noted to carry the traps off. The diet of the wolverine was described to include hares and grouse. Some hunting activities mentioned include attacking disabled deer, and destroying foxes in burrows.

* Dagg, A.I., and C.A. Campbell. 1974a. An annotated bibliography on the status and ecology of the wolverine in Canada. Can. Wildl. Serv. Manuscript Rep., Ottawa. 45pp.

A) 1; B) Canada; C) Literature search and compilation of references.
Population Dynamics - poptrend.
Species Management - harvest.
Other Topics - bibliography.
Comments - It is noted that although the wolverine is largely a Canadian species in North America, it was featured in only 1 "...of 639 articles...on Canadian mammals published over the past 40 years in 14 well-known refereed journals or series..."; the bibliography lists 287 articles, complete with keywords for a variety of biology and management subjects, and including general mammal distribution papers that mention wolverine only briefly or, in some cases, not at all (the negative information apparently considered significant in those cases); only 17 of the listed papers were considered "very useful", and just 6 of those based on observations in North America; appendices include provincial, territorial, and Canada-wide pelt sales for the period 1921-1972, summaries of species status by province and territory, and a summary of museum specimen holdings.

* Dagg, A.I., and C.A. Campbell. 1974b. Historic changes in the distribution and numbers of wolverine in Canada and the northern United States. Unpubl. Rep., Can. Wildl. Serv., Ottawa. 21pp.

A) 2; B) Canada; U.S.A.; C) Literature review.
Description - distribution.
Population Dynamics - poptrend, popcomp.
Species Management - harv/strategy.
Other Topics - history.
Comments - It is believed that "...the wolverine is one of the rarest mammals in Canada, especially in the east", but there is little specific data on its exact distribution and abundance; there are differences of opinion as to whether the species occurs primarily in taiga, tundra, or the transition zone habitat along the treeline, but there appears to be evidence that it formerly occurred farther southward, into broadleaf forest, in both North America and Europe; prehistorically the wolverine occurred in most Canadian provinces, but has apparently always been absent from most islands south of the arctic circle on both coasts--Nova Scotia, Prince Edward Island, Newfoundland, Anticosti Island, Queen Charlottes--(but present on Vancouver Island); the species was apparently extinct in New

Brunswick by about 1850, and its range has shrunk to the extreme north in Quebec, Ontario, Manitoba, Saskatchewan, and Alberta--the geographic range in B.C., Yukon, and N.W.T. is considered to have remained about as in historic times, with possible increases in some of the arctic islands which are reached by ice crossings; in the U.S., wolverines were recorded and possibly resident in at least 22 of the 48 contiguous states, but their range has now shrunk to a small nucleus population in seven western states; estimates of relative numbers, based on harvests and subjective reports, suggest declines in most areas; possible causes listed for the postulated declines are over-trapping and hunting, habitat changes, intolerance to human developments, poisoning during predator control operations, the decline of caribou, reproductive failure due to imbalanced sex ratio and/or reduced numbers, and negative effects of the changing (warming) climate; recommendations for management include hunting and trapping closures in eastern Canada, more intensive harvest monitoring in northern and western Canada, establishment of special parks and/or reserves, transplants, increased public education, captive breeding, and increased research.

* Danilov, N.D. 1965. Some data on the reproduction of glutton. Zool. Zhurnal 44:1737-1739. (Engl. Translation 1117, Foreign Languages Div., Dept. Sec. State, Ottawa. 5pp.)

A) 0; B) USSR; C) Laboratory examination of 2 animals, 1 of each sex.
Population Dynamics - natality.
Comments - Much description and several measurements, but no new knowledge; both specimens were taken in about mid-March, and it was concluded that the male was sexually active and the female in "pro- estrous" at that time.

* Davis, D.G. 1967. A brief note on the birth of wolverines. Internatl. Zoo Yearbook 7:127.

A) 1; B) Montana; C) Observation of captive animals.
Life History - nutrition, behavior, pelage.
Population Dynamics - natality.
Comments - Two young were born at the zoo on 16 February 1965--mating was not observed, so the length of gestation was not known; the young, which were "pure white" at birth, did not emerge from the den until late April, and then only at night; they first came out in daylight in mid- May, at age 3 months, and by that time were in pelage resembling that of the adults.

* De Vos, A. 1964. Range changes of mammals in the Great Lakes region. Amer. Midland Nat. 71:210-231.

A) 0; B) Canada, U.S.A.; C) Literature review.
Description - distribution.
Comments - The wolverine is thought to have had a wide range throughout the Great Lakes region (Minnesota, Michigan, Wisconsin, south and central Ontario, Ohio, Pennsylvania, and New York) prior to arrival of the white man, though in only small numbers, but has been essentially extinct in that area since the early part of the present century.

✈ Ewer, R.F. 1973. The Carnivores. Cornell Univ. Press, Ithaca, New York. 494pp.

A) 1; B) General; C) Literature review.
Description - features.
Life History - food, behavior, denning.
Population Dynamics - natality.
Other Topics - genetics.
Comments - The wolverine is described as "...rather like an over-grown marten"; no original material is presented, but this reference is of interest in providing a translation of several conclusions from Krott (1959a), the source of all following points; the wolverine's year is divided into essentially two seasons--that with snow and that without; carrion and cached food dominates in the winter diet, while small rodents, bird's eggs, wasp nests, and berries are commonly taken in summer; food remaining after a meal is cached, and is important to survival in times when hunting is difficult--ability to locate caches is not limited to ones they made themselves, so raiding of others stores (including those of man) is common; the anal gland secretion is emitted only when the animal is alarmed, while the ventral gland is used for marking; female territories are included within those of males, but are usually exclusive from each other--the size of the territory is believed related both to availability of food and of den sites; wolverines are believed to provide "prolonged post-weaning maternal care" and to breed only every other year; the species diploid chromosome number is given as 42 (the same as the least weasel and 4 more than martens and fishers).

✈ Filinov, C. 1980. Predator prey problems in nature reserves of the European part of the Russian U.S.S.R. J. Wildl. Manage. 44:389-396.

A) 0; B) USSR; C) Long-term field investigations.
Population Dynamics - poptrend.
Species Management - economics.
Comments - Wolverines were listed present in only 2 of 9 nature reserves studied, and those were also the only two reserves supporting reindeer; the estimated densities (km^2/wolverine) for those two reserves, Laplandsky and Pechoro-Ilychsky, were 135-160 (10-12 animals) and 290-360 (20-25 animals), respectively; wolverine predation accounted for 2.4% of all documented natural mortality of moose and 10.2% of natural mortality for reindeer at Laplandsky; comparable figures for Pechoro- Ilychsky were 5% (moose) and 51% (reindeer); wolverine hunted reindeer more than they did other ungulates; it was concluded that predation was not a significant factor for the ungulate populations involved.

* Fry, W. 1923. The wolverine. Calif. Fish Game 9:129-134.

A) 1; B) California; C) Incidental field observations and reports.
Life History - food, behavior.
Population Dynamics - poptrend.
Comments - The wolverine is described as in danger of extinction in the state; it is said to occur in the high Sierra, at elevations of 6500- 13,000' (1975-3950 m), not descending to local lowlands even in winter; foods reported are carrion, yellow-bellied marmots, and smaller rodents such as "gophers" (ground squirrels?), rats, and mice--digging for rodents has been observed; a taste for porcupines, which results in death from quills in internal organs, is described as one of the factors hastening the species' demise, but no documentation is provided; instances of black bears, coyotes, and cougars giving up kills or carrion to wolverines is described in support of the author's label for the species as "king beast of the Sierras"; despite occasional damage to cabins and other property, a case is made for preserving the species.

* Gardner, C.L. 1985. The ecology of wolverines in southcentral Alaska. Unpubl. M.S. Thesis, Univ. Alaska, Fairbanks. 82pp.

A) 3; B) Alaska; C) Field (telemetry) studies and analysis of a small sample of trapped specimens, 1979-82.
Description - features.
Habitat Characteristics - cover.
Life History - food, hmrange, movements, dispersal, socbehav, behavior.
Population Dynamics - mortality.
Species Management - age/tech, harvest.
Comments - Of 12 wolverines instrumented, 10 were males and most field study results apply primarily to that sex; animals were captured by darting from a helicopter, as trapping proved unsuccessful; **HOME RANGE AND TERRITORIALITY** - mean winter and summer home ranges for adult males were 353 km^2 and 385 km^2 respectively; the one male tracked for an entire year had winter and summer ranges of 515 km^2 and 451 km^2, respectively, and a total annual range of 637 km^2; there was little range overlap between adjacent animals, except between an adult and a juvenile, the latter eventually dispersing from the area; the summer range of a lactating female with 2 kits was 92 km^2; the Susitna River acted as a home range boundary for 6 of 7 males, but was not a barrier to their movement; **MOVEMENTS** - distinct seasonal shifts in elevation occurred, with animals moving up in spring (apparently mostly to hunt emerging ground squirrels) and down in late fall/winter to ungulate winter ranges; animals moved about regularly, but occasionally concentrated activity in one area for a period; the two factors leading to intensive local use were presence of a large carcass (used up to 27 days in one case) and breeding (pairs remaining together in a localized area 2-3 days); one carcass was used concurrently by a juvenile and adult male, with both there together in at least one occasion; **DISPERSAL** - two documented dispersals involved a 2-year old male that moved a minimum of 378 km, where it was trapped in the Yukon, and a juvenile male that moved 30 km before it was trapped; **HABITAT** - spruce communities and ecotonal areas (mostly rock outcrops) were

used significantly more than in expected in relation to availability--winter ground tracking showed that even though animals might be located in all habitats, they were not all of equal significance--they appeared to be coursing and hunting primarily in the spruce types and making straight- line movements (traveling) through tall shrub and deciduous forest communities; tundra communities were avoided in winter; FOOD HABITS - chief winter food items (colon analyses, N=35) by frequency and percent dry weight were moose (24.7, 41.1), caribou (20.0, 20.4), microtine (20.0, 6.7), and bird (11.4, 1.7); moose was the most common ungulate present, especially in winter, and most use appeared to be at wolf kills; among small mammals, red squirrel (8.6, 1.7), snowshoe hare (5.7, 0.8), porcupine (2.9, 1.7), and "beaver/muskrat" (2.9, 10.6) were also commonly used, and soil was a regular and large component (20.0, 15.4); caching and use of caches was not commonly recorded--wolverines and foxes often followed each other's tracks, probably looking for cached prey; summer food was believed to be chiefly ground squirrels, birds, and microtines; FEATURES - the average live weight for 10 males of all ages was 15.8 kg (range 14.1-17.7), and for 2 females was 10.0 (9.5- 10.0); MORTALITY - a male that died of undetermined "natural causes" was mostly eaten and the remains cached by another wolverine, apparently in late winter (found in mid-April); the most important mortality factor appeared to be harvest by humans, which apparently focussed primarily on juveniles: HARVEST - the recorded local harvest during 3 seasons was 103 males:73 females (1.4:1), a significant difference; most of the harvest was in February and March--males, especially the two immature classes, dominated in December, with females increasing in the harvest later on; AGE DETERMINATION involved use of dental cementum, with the canine believed to give better results than other teeth; AGE COMPOSITION of the local sample included 22 kits (43%), 15 subadults (29%), and 14 adults (28%); MANAGEMENT CONSIDERATIONS - analysis of the harvested sample plus the fact that 6 of 10 of the captured animals were adults was taken to indicate that the population was not being heavily harvested; it is noted that census of wolverines is not presently feasible and will not likely be in the near future, and that analysis of harvest samples can detect population changes (primarily composition) only after the fact.

* Gardner, C.L., W.B. Ballard, and R. H. Jessup. 1986. Long distance movement by an adult wolverine. J. Mammal. 67:603.

A) 2; B) Alaska, Yukon Territory; C) Incidental field observation.
Life History - dispersal.
Comments - A radio-collared adult male wolverine (2 years old, 18.0 kg), after spending a minimum of 19 days within the home range of an older (7 year old) resident male in southcentral Alaska, left the area and was trapped about 20 months later in the Yukon, 378 km to the east.

Gardner, C., W. Ballard and R. Jessup. 1986. Long distance
** movement by an adult wolverine. Journal of Mammalogy 67(3):603.

A two year old male wolverine was captured and radio-collared from the Susitna River in southcentral Alaska. For at least 19 days it used the same home range area as the known resident 7 year old male. After 19 days the signal was lost, and this wolverine was not recovered until it was trapped 1 year and eight months later along the White River in Yukon Territory, Canada. The distance traveled was equal to a straight line distance of 378 km.

Groves, C.R. 1987. Distribution of the wolverine (Gulo gulo) in
** Idaho, 1960-1987. Idaho Department of Fish and Game. Boise. 24 pp.

This paper provides historical documentations of wolverines in Idaho and results from the 1985 mail questionnaire survey (Groves 1988). Researchers suggest the wolverine maybe more common than once thought because of increased access and human interest in remote areas where wolverines occur.

Groves, C.R. 1988. Distribution of the wolverine in Idaho as
** determined by a mail questionnaire. Northwest Science 62(4):181-185.

To determine the current (last 25 years) distribution of wolverine in Idaho, mail questionnaires were sent to biologists and trappers in Idaho. Biologists were asked to answer the following questions: date, location (place name, county, longitude/latitude or township-range-section), habitat type, type of observation (animal, track, or scat). They were also asked to provide the name, address, and phone number of other people who have sighted wolverines in Idaho. Trappers were sent a cover letter and an addressed, postagepaid post card.
Questions on the card included: name, address, phone number, their general trapping area, 'yes' or 'no' if they had trapped or seen a wolverine or sign in the past 25 years. If 'yes' the date and area were requested. Follow up telephone calls were made to biologists and trappers who responded 'yes'. Confirmed reports consisted of photographs or a carcass. Respondents filing reports not fulfilling these qualifications were asked to describe the animal, their level of confidence of the observation, if they had previously observed a wolverine, distance and duration of observation, and their amount of experience as a biologist or trapper. Reports by respondents who lacked confidence of their observation, poorly described the animal or observed it for a short duration and/or at a great distance were not considered a confirmed sighting.

The returns rate were 62.5 % for biologists and 28.5% for trappers.

The survey resulted in 10 confirmed, and 89 probable sightings. Of the ten confirmed 8 were from northern Idaho (north of Lochsa River), eight were from National Forest land, 5 were from 1960-1975, and 5 were from 1976-1986. Groves suggests this method is good for providing information about distribution but not population viability or size.

Groves, C. and G. Gadwa. 1989. Status survey for wolverines (Gulo
** gulo) on the Sawtooth National Forest and adjacent areas. Idaho Department of Fish and Game. Boise.

Hair traps, mail questionnaires and a poster describing wolverines and requesting sighting information were used as a winter survey technique to determine the status of wolverines on the Sawtooth National Forest and adjacent areas. Recommendations for management as a Forest Service sensitive species are provided.

See Groves (1988) for a more detailed account of their mail questionnaire method. While setting hair traps, researchers located wolverine tracks which appeared to be following a marten trap line. Locations of additional tracks suggest that wolverines were using habitat types dominated by lodgepole pine (Pinus contorta), near stream bottoms in mid to lower elevations. Although wolverine fur was not found in hair traps, researchers reserved judgement on the use of hair traps during this survey because of small sample size and lack of time available to check traps. Reported sightings seem to have a direct correlation with areas of easy access. Out of 24 reported sightings only one was "confirmed" by a photograph.

* Haglund, B. 1966. Winter habits of the lynx (*Lynx lynx* L.) and wolverine (*Gulo gulo* L.) as revealed by tracking in the snow. Viltrevy 4:81-299.

A) 2; B) Sweden; C) Snow-tracking, winters of 1960-64.
Habitat Characteristics - vegetation.
Life History - food, activity, movements, behavior, socbehav, denning.
Species Management - economics, interactions.
Comments - A total of 957 km of wolverine trails was followed, mostly in late winter (March and April); during winter "...most of the wolverines live in the low mountains or in the coniferous forest bordering on the high mountains"; daily activity is irregular, showing no distinct pattern--the species is described as the most likely of the four large European predators to be seen in "bright daylight"; daily movements were difficult to determine

because of the irregular activity pattern, but "...a normal distance seems to be at least 30 km"; the primary winter food was reindeer, occurring in 32 of 38 scats (84%)--other scat occurrences were rodents in 10 (26%), and a variety of plants fragments and bone material; the small mammals in the scats included 22 individuals--18 lemmings, 2 unident., 1 vole, and 1 shrew; of 50 reindeer kills visited by wolverines, it was believed that 15 had actually been killed by the wolverines and at least another 20 by lynx-- wolves are rare in the area and lynx are said to have taken over that species role of providing meat for wolverines; wolverines are unskillful hunters, chasing prey when the opportunity presents itself but doing so clumsily--none of 7 chases of hares or tetraonids were successful, and pursuits of reindeer were successful only in late winter when snow conditions favored the wolverine and (possibly) when the reindeer were in poorest physiological condition; attacks were usually on the backs of prey animals, with bites directed to the neck and/or spine; the wolverine was considered less likely than other predators to take prey in prime condition; wolverines showed a particular interest in lynx tracks in early winter (before March), following them an average of 5 km when they were encountered, but showed little interest in them in March and April when numerous carcasses were available--the distance between carcasses was 23.9 km before March, 8.7 km in March, 12.9 km in April, and 7.1 km in May; food storage (caching) is a conspicuous part of the wolverine's behavior, and is accomplished most often by digging it down into the snow; occasional removal of a prey animal's head was noted; territorial marking by biting into small trees and by deposits of urine and feces were noted; wolverines were mostly solitary in winter, but there were several records (particularly in late March) in which two adults, believed male and female, traveled together for a time; natal dens were most commonly snow caves amid rock formations in the mountains, but "...might be found below the limit of coniferous forests...usually among the rocks...below a mountain slide"; there was some indication that natal denning areas were selected in areas where stored carcasses had accumulated.

* Haglund, B. 1974. Moose relations with predators in Sweden, with special reference to bear and wolverine. Naturaliste Can. 101:457-466.

A) 0; B) Sweden; C) Review of literature and anecdotes.
Life History - food, behavior.

* Hash, H.S. 1987. Wolverine. Pages 575-585 *in* M. Novak, J.A. Baker, M.E. Obbard, and B. Malloch (eds). Wild furbearer management and conservation in North America. Ontario Trappers Assoc., North Bay.

A) 2; B) General; C) Literature review.
Description - features, distribution, taxonomy.
Habitat Characteristics - vegetation, cover.
Life History - lifehist, denning.
Population Dynamics - mortality, natality, poptrend.
Species Management - census, economics, harv/strategy, transplants.
Other Topics - history.

Comments - This is an excellent review of wolverine biology and management, including results from all significant studies through 1985, but because it largely draws on literature described in detail in the present annotated bibliography, it will not be extensively quoted--only new information and/or unique interpretations follow; the point is made that the northward diminution of the historical range on this continent commenced in the mid-1800's, coincidental with increased European exploration and settlement and expansion of the fur trade, and decline of the northern bison; the boreal forest, most of which is remote and little affected by development, is presently "...the largest geographic area of occupied wolverine habitat"; two pregnant females recently killed in early March in Montana contained fully developed fetuses, and "several" litters 2-3 weeks old have reportedly been observed in that state in March; natal dens in Montana are most commonly associated with snow-covered tree roots, logjams, or rocks and boulders; wild wolverines harvested in Montana rarely exceed 8 years of age, and the average is 4- 6; a 1937 reference from California is cited as reporting that dead wolverines had been found with their stomachs and digestive tracts impacted with masses of porcupine quills; population assessment may be best accomplished by use of indirect indices, with use of bait stations to attract animals; reintroduction to areas of former habitat is recommended to assist in population recovery--releases in the ratio of 2-4 females per male is recommended; "Carefully regulated harvest programs, the implementation of refined monitoring techniques, appropriate reintroduction programs, and the preservation of adequate suitable habitat should ensure the survival of the wolverine for future generations."

* Hash, H.S., and M.G. Hornocker. 1980. Immobilizing wolverines (*Gulo gulo*) with ketamine hydrochloride. J. Wildl. Manage. 44:713-715.

A) 1; B) Montana; C) Field testing of the drug.
Description - features.
Species Management - gen/tech.
Comments - Ketamine administered in dosages of about 20 mg/kg body weight produced satisfactory results with no mortalities in 24 immobilizations; onset of immobilization occurred in an average of about 4 minutes for both sexes; males were immobilized for shorter periods (about 30 vs. 45 minutes), and recovered more quickly than females; gentle handling and holding in an enclosure until complete recovery (several hours) is recommended.

Hatler, D.F. 1989. A wolverine management strategy for British Columbia. Wildlife Bulletin No. B-60, B.C. Ministry of Environment, Victoria, B.C. 124pp.

Bibliography and literature review
British Columbia

An excellent and complete literature review of wolverine biology and management, this report includes a very usable, cross referenced annotated bibliography.

* Haugen, A.O. 1961. Wolverine in Iowa. J. Mammal. 42:546-547.

A) 1; B) Iowa; C) Report of an animal shot, May 1960.
Description - features, distribution.
Life History - food, health.
Comments - An adult female wolverine, weighing 22 lbs (10.0 kg), was pursued and shot in a cornfield; the animal had badly worn teeth and 2 or more toes missing from 3 of its feet (those wounds well healed), suggesting several past encounters with traps; the animal showed no sign of recent pregnancy; stomach contents included carrion (probably cow), and shells from ground-nesting birds, including pheasant; parasites found included 23 ascarids (*Physaloptera* spp.) among the viscera and *Trichinella* larvae in a muscle tissue sample; the author was doubtful that the animal had arrived in Iowa under its own power, but had no certain information to the contrary.

* Hoak, J.H., J.L. Weaver, and T.W. Clark. 1982. Wolverines in western Wyoming. Northwest Sci. 56:159-161.

A) 1; B) Wyoming; C) Compilation of sightings from interviews and voluntary reports.
Description - distribution.
Population Dynamics - poptrend.
Comments - A total of 50 records, 5 involving more than one animal (including family groups), were assembled for the area of western Wyoming outside Yellowstone National Park in the 1960's and 1970's; the increased number of sightings in comparison to 4-5 decades previous is thought to be the result of "...increased human use of remote areas, an extension of wolverine range, or both"; the ban on use of poisons for predator control on federal lands is considered beneficial to carrion feeders such as the wolverine.

* Holbrow, W.C. 1976. The biology, mythology, distribution and management of the wolverine (*Gulo gulo* L.) in western Canada. M.N.R.M. Practicum, Univ. Manitoba, Winnipeg. 214pp.

A) 2; B) Canada; C) Review of literature and anecdotes.
Description - distribution.
Life History - lifehist.
Population Dynamics - poptrend.
Species Management - economics, harv/strategy.
Other Topics - history.
Comments - In its compilation of wolverine lore, legend, and anecdotes, this document is second to none, but the review was undertaken prior to any significant field studies on the species on this continent--only new or unique information, not described elsewhere in the present bibliography is given below; an unpublished winter tracking study in Mt Assiniboine Prov. Park, B.C. (Cockerton and Herrero 1973) reported movements of 25 km...in several hours, 25-30 km in another case, and 120 km in a third...with no obvious

signs of rests or pauses"; a wolverine shot in a mining camp in the Northwest Territories was apparently dragged away by another wolverine within two hours, and portions of it were eaten in the approximately 5 km the tracks were followed, until the remains were left behind; trapper activity and wolverine population status information was obtained by interviews and questionnaires for Manitoba, Saskatchewan, Alberta, British Columbia, Yukon and Northwest Territories--only significant information and interpretations for B.C. are given below; of 156 B.C. respondents to a questionnaire for trappers, 104 (67%) had set traps specifically for wolverine--for the entire western Canada study area, the figure was 182 of 344 (53%); most B.C. trappers (56 of 72 = 78%) used killer traps (mostly conibears, deadfalls, or snares) when setting for wolverine; changes in wolverine abundance in B.C., as indicated by harvest returns and sightings records, "...are much less pronounced than (for) any other province or territory in the study area"; one trapper from the Stewart area of B.C. noted that after January he takes no female wolverine (implying that they had disappeared by then...); fur production records do not support the contention that wolverines have a 10-year cycle, and most trappers did not believe that to be true--it was noted, however, that the animals might appear on a trapline one year and not the next; the species is not overly important economically--one trapper noted that "If a guy had to depend on...all the wolverine he caught, he'd be one hungry S.O.B..."; wolverines have often been trapped because of their reputation for damage or as predators rather than for fur value; although generally ranked as the most damaging species on a trapline (slightly ahead of wolf), total annual damage estimates by trappers were about $250 (with only a portion of that due to wolverines); further, only 128 of 394 trappers (32%) had ever experienced damage by wolverines (63 of 178 = 35% in B.C.), and only 31 of 153 (20%) felt that wolverines were a negative influence on the local fur industry (13 of 54 = 24% in B.C.); termination of the open season for hunting throughout B.C., and closed seasons for trapping in several areas of the province are recommended.

✱ Hornocker, M.G., and H.S. Hash. 1981. Ecology of the wolverine in northwestern Montana. Can. J. Zool. 59:1286-1301.

A) 3; B) Montana; C) Field studies, including live-trapping and marking, snow-tracking, and telemetry, 1972-1977.
Habitat Characteristics - study/area, cover.
Life History - food, hmrange, movements, dispersal, socbehav, behavior.
Population Dynamics - natality, mortality, poptrend, popcomp.
Species Management - gen/tech, harv/strategy, refuges.
Habitat Management - forestry, hab/strategy.
Comments - This was the first intensive field study of wolverines in North America, and detailed coverage here is warranted; it is noted that within the contiguous 48 states, only Montana had "...adequate numbers to constitute viable populations"; a total of 24 different individuals were captured and marked during the study, including 11 males (9 adults and 2 subadults) and 13 females (8 and 5); **FOOD HABITS** - large wild and domestic ungulates, all believed taken as carrion, predominated in 56 winter scats collected during the study

period, with deer or elk in 15 (27%), domestic cow in 15 (27%), and horse in 10 (18%); other food items identified, and frequencies, were snowshoe hare (9 occurrences, 17%), marmot (6, 11%), beaver (3, 6%), small rodents (3, 6%), birds (3, 6%), and porcupine (2, 4%); food caching was not a conspicuous feature of wolverine behavior on the study area, and it is speculated that it may be important in population dynamics "...only in areas where other scavenging species are scarce and where permafrost exists; incidence of marmot in winter scats was believed to represent predation on hibernating animals; Columbian ground squirrels were abundant in some areas frequented by wolverines, especially in spring when they are believed particularly vulnerable to predation, and it is believed that "...wolverines preyed heavily on the squirrels"; **MOVEMENTS** - mean movements between relocations of radio-collared animals were greatest during spring and summer, and greater for males than for females-- maximum 3-day movements were 64 km for males and 38 km for females; **HOME RANGE** - mean home ranges for males and females, respectively, were 422 and 388 km^2--lactating females showed reduced spring and summer ranges (about 100 km^2); individuals of both sexes showed fidelity to particular areas, but some made long movements away from those areas for periods of up to 30 days; **HABITAT** - both sexes used higher elevation habitats in spring and summer than in winter--mean elevation of radio- locations during the 4 seasons were winter -1371 m, spring - 1676 m, summer - 1920 m, and fall - 1889 m; all aspects were used, but "...easterly and southerly areas received the majority of consistent use"; 70% of all relocations were in medium density or scattered mature timber, while most of the rest were in ecotonal areas--dense young timber, burns, and wet meadows were rarely used; "wet timber, dry timber, and alpine areas composed 23, 31, and 16%, respectively, of all relocation sites; wolverines selected *Abies* forest types, occurring there in 56% of locations despite the fact that it constituted only 27-42% of available cover--that selection was particularly pronounced in summer; no wolverines were relocated in clear cuts of any size, although tracks crossing clearcuts were observed 15 times--tracking showed that "...wolverines meandered through timber types, hunting and investigating, but made straight line movements across large openings" (usually at a lope or gallop); bed sites were often in snow on open outcrops "...all in timber types which afforded cover"; geographic barriers such as mountains and large rivers do not confine wolverine populations as they do other species, therefore the populations "...must be treated as regional rather than local"; **NUMBERS** - a minimum of 20 wolverines were estimated for the 1300 km^2 study area, for a density of 1 animal/65 km^2--that density is higher than reported elsewhere, possibly because of the high density and diversity of available ungulates in the area; **MORTALITY** - 18 mortalities were recorded during the study, including 15 animals taken by trappers (9M, 5F, 1U--5 of the 15 marked) and 3 collared animals dying of "natural causes"; the natural deaths included an apparently "old" female that was diagnosed as dying from a uterine infection, and two animals (an old male and a subadult female) that apparently died of starvation--both relied heavily on trap baits before death, and were captured repeatedly; one female wolverine sustained injuries believed to have been caused by a mountain lion, and many of the captured adults were missing toes and/or had broken teeth, probably indicating encounters with traps; **REPRODUCTION** - of 15 female reproductive tracts in preimplantation condition, a mean of 2.93 corpora lutea were found and among 6 tracts with implanted embryos or fetuses the

mean number was 2.17, suggesting that "...productivity in our area may be lower than in Alaska"; capture-recapture data indicated that females did not produce young every year and it was believed that "...no more than half the females present...were reproductively active in each of the 5 years..."; DISPERSAL - kills from outside the study area indicated that dispersal of young from the area occurred; TERRITORIALITY - range overlaps between and among the sexes were common and territorial defense was not apparent--it is speculated that the observed pattern reflects either the animal's scavenging life style (in which flexibility of movement is required and maintenance of a large exclusive area would be difficult), or the fact that turn-over in the population was too rapid to enable individuals time to develop their full territorial system; MANAGEMENT CONSIDERATIONS - wolverines used "wilderness" and "non-wilderness" areas equally, but were in the nonwilderness (logging and recreation area) primarily in winter, when human activity there was least, and were high in adjacent, rugged mountains during much of the snow-free season; the wolverine has long been regarded as a pest over most of its range, and its relatively low fur value has resulted in its not being a priority for conservation, but in 1975 Montana removed the "predator" classification and introduced more stringent harvest regulations including a distinct trapping season and a season limit of 1 animal per trapper--the annual take has "declined markedly" as a result; "wolverines come readily to bait and are vulnerable to skilled trappers" and it is therefore recommended that "...bait trapping for all species...be curtailed" where enhancement of wolverine populations is the goal; it is also recommended that seasons be closed during the late winter and early spring when the young are born; "Wolverine populations in northwestern Montana survived the years of unlimited hunting and trapping solely because of the vast expanses of official wilderness and remote, essentially wilderness habitat..." (which) "...functioned as both refuge and reservoir for wolverine populations."

* Hornocker, M.G., J.P. Messick, and W.E. Melquist. 1983. Spatial strategies in three species of Mustelidae. Acta Zool. Fennica 174:185-188.

A) 2; B) Montana; C) Literature review.
Life History - dispersal, socbehav.
Comments - Wolverines marked profusely, but displayed little territorial defense by aggression; individuals showed fidelity to particular areas, but occasionally left them, apparently mostly in response to food availability considerations; young animals dispersed long distances, up to 150 km recorded, and males made seasonal movements during the breeding season; "The scavenging lifestyle of this species dictates long seasonal movements, a relatively large home area, and a solitary existence"; strict maintenance of territories would be difficult, given their large size, and would not seem advantageous to a species largely dependent on carrion--"a system which provides for flexibility of movement to areas of carrion abundance would appear to be more successful"; it is concluded that the three species (wolverine, otter, badger) have a flexible behavioral system that "...may be regarded as a positive adaptation to different and changing environments and is of value to the species' survival"; "From our data, we would expect to encounter different spatial strategies in any of these three Mustelidae anywhere, with this strategy wholly dependent upon external and internal influences acting on any particular population."

* Houston, D.B. 1978 . Elk as winter spring food for carnivores in northern Yellowstone National Park, Wyoming, U.S.A. J. Appl. Ecol. 15:653-662.

A) 1; B) Wyoming; C) Monitoring of elk mortality and use of carcasses.
Description - distribution.
Life History - food.

Johnson, C.S. 1990. Re-evaluation of the status of the wolverine in Manitoba. Tech. Rep. No. 90-1. Manitoba Dept. of Natl. Resources, Wildlife Branch.

Status review
Manitoba

ABSTRACT
The status of the wolverine (*Gulo gulo*) in Manitoba in 1990 was re-evaluated in comparison to 1972, recent historical sales records and trapper questionnaires were evaluated to determine the present status. The wolverine population was estimated between 500 and 800 animals. Re-population of some of its former range was attributed to cessation of predator poisoning, increase in the wolf (*Canis lupus*) population and a shortened trapping season. Management recommendations included biological studies and considered the role of carnivores in big game management.

Johnson, R.E. 1977. A historical analysis of wolverine abundance
** and distribution in Washington. Murrelet 58:13-16.

This paper presents historical records of wolverines based on photographs, specimens, sightings and tracks, from 1890-1975. The author implies that the wolverine has made a comeback in regions of Washington, especially in the northeast. Two distribution maps (1890-1959 and 1960-1975) are provided.

Johnson, V. 1990. Wolverine. IN: D.C. Zeiner, W.F. Laudenslayer,
** K.E. Mayre, and M. White, editors. California's wildlife volume III, Mammals. California Fish and Game.

This paper an account of wolverines in California. Wolverine are state threatened and fully protected. In addition, distribution, abundance, habitat, and other life history information is discussed.

* Kebbe, C.E. 1966. Wolverine killed in Oregon. Murrelet 47:65.

A) 1; B) Oregon; C) Report of an animal killed, September 1965.
Description - features, distribution.
Comments - The large male, weighing 28 lbs (12.7 kg), constituted the first specimen record since 1912; reference is made to "...several unverified reports....in the last five years" which indicate that a remnant population may still exist in remote areas of the Cascade Range.

* Kelsall, J.P. 1981. Status report on the wolverine, *Gulo gulo*, in Canada in 1981. Comm. Status Endangered Wildl. Can., Ottawa. 47pp.

A) 2; B) Canada; C) Literature review and interview of government wildlife managers.
Description - taxonomy, distribution.
Life History - lifehist.
Population Dynamics - poptrend, popreg.
Species Management - harv/strategy, transplants, refuges.
Comments - This is an excellent review of then existing information; fur harvest and sightings data suggest declines in overall numbers in the past decade, and that result may be related to increased pelt prices; "the primary limiting factors are believed to be predation by humans, reduction of habitat by encroaching civilization, and availability of food, particularly carrion from large ungulates, in winter"; included among "predation by humans" is the incidental kill of wolverines by past wolf poisoning programs (1 wolverine per 8.9 wolves documented at bait stations in northern Canada); harvest regulations in the various Canadian jurisdictions are reviewed--most are liberal, and some significance is attached to the fact that open seasons are maintained during the whelping season; up to 50% of the wolverine pelts sold annually in Canada in recent decades have come from British Columbia; knowledge of the species is considered "insufficient to recommend sound management measures", and the major recommendations are for increased research and monitoring; it is concluded that "as a scavenger on the peripheries of the food web, requiring huge areas of wilderness as home range, the wolverine does not lend itself readily to direct management programs"; maintenance of important food resources, particularly the large caribou herds of the north and the diverse ungulate faunas of the western mountains and large national parks is considered fundamental to maintenance of wolverine populations in Canada.

** Koehler, G.M. 1990. Winter survey for wolves and wolverine on the Clearwater National Forest - 1989-90. Order Number 43-0276-9-0505 Wildlife Research Institute. Moscow, Idaho.

This survey took place along major drainages, at lower elevations where ungulates congregate. Tracks and other sign were searched by personnel on snowmobiles or skis. Snowmobile speed was limited to 20 mph, so sign was not missed. Tracking occurred after

snowfall. Routes were surveyed at least once in early winter and once in late winter. Ungulate carcasses were examined for cause of death and other sign. After surveying 638 miles of routes, only one set of wolf and one set of wolverine tracks were located. The wolverine tracks were found at Musselshell Creek (T35N R6E S7). Both species may be "rare" or "uncommon" on the Clearwater National Forest.

* Koehler, G.M., M.G. Hornocker, and H.S. Hash. 1980. Wolverine (*Gulo gulo*) marking behavior. Can. Field-Nat. 94:339-341.

A) 2; B) Montana; C) Field observations, snow-tracking.
Life History - socbehav.
Comments - Four types of scent marking were observed: 1) deposition of musk on a tree trunk or on the ground, 2) scratching the ground (with or without musk deposition, 3) gnawing or biting a limb or root scented with musk, and 4) deposition of scat or musk on the ground without leaving visual signs; the first type, which usually involved climbing the tree, comprised 70% of 157 recorded marking sites; musk was seen and smelled on trunks an average height of 46 cm and as high as 74 cm from the base; one wolverine marked 20 different sites in 2.5 km of travel; marking sites tended to be on prominent trees in an area, but sometimes were on scats left by other species (e.g., coyotes), hummocks of snow, small trees, and rocks; some sites were known to have been marked by at least two different individuals; males were documented marking on 4 occasions, but no positive evidence of female marking was obtained; it is speculated that marking may be useful primarily for maintaining time rather than area spacing--i.e., indicating an area is occupied and facilitating avoidance by others; from the energy expended and attention given, it is concluded that marking behavior is an important form of communication among wolverines.

* Kovach, S.D. 1981. Wolverine, *Gulo gulo*, records for the White Mountains, California. Calif. Fish Game 67:132-133.

A) 1; B) California; C) Literature review and report of an incidental field observation.
Description - distribution.
Comments - A total of three sight records over a 40 year period (1937, 1960, and 1977) are cited as indicating that the Sierra Nevada Range may not be the only mountains used by wolverines (past and present) in California; the most recent sighting, in early July, involved two animals of somewhat different sizes that went under a boulder (possible den site) on a talus slope.

* Krott, P. 1960. Ways of the wolverine. Nat. Hist. 69:16-29.

A) 3; B) Sweden; C) Observations of both wild and free-ranging captive animals.
Habitat Characteristics - cover, climate.
Life History - food, activity, socbehav, behavior.
Population Dynamics - natality.
Species Management - interactions.
Comments - This is a unique perspective on behavioral attributes of the species, which is considered uniform throughout its circumpolar range; its primary habitat is listed as "swamp areas of the northern coniferous forest region", to which it has become "ecologically bound" through its relationship with the wolf--the wolf is believed to largely exclude the wolverine from firmer ground and more open areas (in summer) both by competition and predation; the species is territorial, with boundaries marked by glandular secretions, urine, and feces and respected by other individuals; foods, in addition to carrion include eggs of ground nesting birds, wasp larvae, and berries--the animal functions as a predator of larger mammals only in winter, when snow conditions provide an advantage; despite its reputation for voracity, it shows no particular interest in new food opportunities after it has already eaten; a conspicuous feature of wolverine feeding behavior is caching of remains, usually by burying in snow or underground, but sometimes by wedging among branches of a tree; the species is not strictly diurnal or nocturnal--rather, it tends to be active for 3-4 hours and then at rest for a similar period, that pattern occurring in a more or less continuous cycle--bad weather (heavy snowstorms or rainfall) may result in longer periods of rest (up to days) and certain favorable weather conditions and/or extreme hunger may prolong activity for long periods; the age of sexual maturity is given as 4 years, and females are believed to breed only every 2-3 years, keeping the young with them until the age of 2 years; the havoc created in trappers' cabins and caches is relegated to "play", for which the species is ascribed a tendency approaching that of otters; other behavioral features of relevance to management include a very cautious and suspicious nature, and the ability to learn and change behavior as required--reference is made to the species "...extraordinary ability to evade dangers...(which is)...far superior to any other northern mammal, including the wolf" and to a "considerable immunity to poison" with the animals able to withstand strong doses of strychnine; it is concluded that "...we detest most what we cannot subdue. All the superstition of the north regarding the wolverine can be attributed to ...(its) apparent invincibility."

* Krott, P., and C. Gardner. 1985. Wolverine breeding behavior in Alaska. Saugietierk. Mitt. 32:87.

A) 1; B) Alaska; C) Incidental field observations.
Life History - behavior.
Population Dynamics - natality.
Comments - not seen; cited in Banci (1987).

Kucera, T.E., and R.H. Barrett. 1991. Cooperative wolverine study; first annual report. Dept. of Forestry and Natural Resources, Univ. Calif., Berkeley.

Annual report of field study
California

This report documents efforts during first year of a study designed to assess the presence of wolverines in California. Photographic bait stations were set up in three areas of historic wolverine range and were monitored for a total of 226 camera-nights during the summer of 1991. Black bears, ringtails, turkey vultures, opossum, spotted and striped skunks, and a domestic dog were photographed, but no wolverines were recorded. Researchers were discouraged that bears, in particular, took baits before a wolverine would have a chance to find it and be recorded. They decided to continue the effort in the winter when wolverines were more likely to take baits, and bears would be hibernating.

* Kurten, B. 1970. The neogene wolverine *Plesiogulo* and the origin of *Gulo*. Acta Zool. Fenn. 131:3-22.

A) 0; B) Holarctic; C) Examination of museum specimens and literature review.
Description - taxonomy.
Other Topics - paleontology, evolution.
Comments - Allometric comparisons indicate that the extinct *Plesiogulo* of Asia shows skeletal features intermediate between martens and wolverines, and that "a descent of *Gulo* from *Plesiogulo*, and of the latter from marten-like ancestors, is indicated".

* Kurten, B., and R.L. Rausch. 1959. Biometric comparisons between North American and European mammals. I. A comparison between Alaskan and Fennoscandian wolverine (*Gulo gulo* Linnaeus). Acta Arctica 11:1-20.

A) 1; B) Holarctic; C) Examination of museum specimens (skulls).
Description - taxonomy.
Other Topics - paleontology, zoogeography, morphology.
Comments - Statistical comparisons of skull and dentition dimensions show that the existing Palearctic wolverine has a somewhat larger skull and smaller teeth than its Nearctic counterpart, but the two forms are sufficiently different for taxonomic separation only at the subspecies level--the applicable names are *Gulo gulo gulo* (L.) and *G. g. luscus* (L.), respectively; the difference between the fossil (Pleistocene) wolverine of Europe and recent

(existing) form of North America was actually less marked than that between the fossil and living forms of Europe, and fossil (late Pleistocene) wolverines of North America are essentially identical to their living descendants; it is hypothesized that *luscus* is a relatively late immigrant, perhaps during the late Illinoian, and that most of the differentiation between the two living subspecies is a result of postglacial evolution.

* Liskop, K.S., R.M.S.F. Sadleir, and B.P. Saunders. 1981. Reproduction and harvest of wolverine (*Gulo gulo*) in British Columbia. Pages 469-477 *in* J.A. Chapman and D. Pursley (eds). Worldwide furbearer conference proceedings, Aug. 3-11, 1980, Frostburg, Maryland.

A) 1; B) British Columbia; C) Laboratory examination of specimens.
Description - distribution.
Population Dynamics - natality.
Species Management - harvest.
Comments - It is noted that the wolverine originally occupied all of the province except the Queen Charlotte Islands and "the Vancouver area"; the specimen material included 40 females and 44 males collected from trappers in "northwestern B.C." (boundaries and distribution not given) over a 3-year period, 1976-1979; most of the females were apparently young, either 1-year old (n=16), or 2 (n=13); none of the 1-year olds was sexually mature, but apparently all but 2 of the 2-year olds and all older animals were; 3 of the older animals, aged 5-7, were judged to be "non-reproductive, showing neither corpora lutea nor placental scars; among the 23 females showing reproductive activity, all of 4 taken in November and December, 4 of 5 in January, 1 of 9 in February and 1 of 5 in March were in a pre-implantation condition; the one exception in January had apparently already given birth, while 5 of 8 in February had uterine embryos and 3 were post-partum, and all the remaining March animals (4) were post-partum; among males, 4 of 14 1-year olds, 7 of 11 2-year olds, and all of the older animals were considered mature; some signs of early spermatogenesis (January - March) were found in 3 males; provincial harvests averaged 200-300 animals from about 1920 through the mid-1960's, then increased to 5-year averages of about 400 by the mid- to late 1970's; it is implied that increased harvests might be related to increasing pelt prices since the mid-1960's, although the stated conclusion is that the harvest increase, particularly in the 1970's, "...is probably due to increased accessibility."

* Long, C.D. 1987. Intraspecific communication of the wolverine. Page 13 (abstract only) *in* Townsend, B. (ed). Abstracts of the Fourth Northern Furbearer Conference, 3-4 April 1987, Alaska Dept. Fish and Game, Juneau, Alaska.

A) 1; B) General; C) Observation of captive specimens.
Life History - socbehav, behavior.
Comments - Observations designed to "...ascertain the species' methods and mechanisms of communication" were carried out during 679 diel activity periods of captive animals (4 males, 5 females); it is concluded that scent marking by urination is the primary method of communication--comprising 79% and 87% of all scent marking occurrences recorded for males and females, respectively; abdominal rubbing was second (17% and <1%); all occurrences of anal musking were "trauma induced", indicating it is primarily a fear/defense mechanism; two kinds of vocalizations were described, "chuckling" and "growling".

* MacDonald, D.W. 1983. The ecology of carnivore social behavior. Nature 301:379-384.

A) 1; B) General; C) Literature review.
Life History - socbehav.
Comments - It is speculated that in "less sociable species" such as the bobcat, short-tailed weasel, and wolverine, where several exclusive female territories may be contained within that of one male, female spatial organization may be determined by the distribution of food resources while that of the males is determined primarily by the distribution of females--under the general subject of carnivore social behavior, this pattern is labelled "females as a resource".

* Magoun, A.J. 1985. Population characteristics, ecology, and management of wolverines in northwestern Alaska. Unpubl. PhD Thesis, Univ. Alaska, Fairbanks. 197pp.

A) 3; B) Alaska; C) Field studies, including telemetry, 1978-81.
Description - features.
Habitat Characteristics - study/area, vegetation.
Life History - food, hmrange, movements, dispersal, socbehav, behavior, health, denning.
Population Dynamics - natality, mortality, poptrend, popcomp, popreg.
Species Management - repro, harvest, harv/strategy.
Comments - The study area was north of the treeline, in arctic tundra, where a wind chill factor of -31° C occurs 50% of the time from December through February; absence of vegetative cover facilitated regular observation of the wolverines; caribou are abundant in the area in summer, but there are no large ungulates present in winter; AGE DETERMINATION - a variety of features were evaluated to assign field age, including tooth wear and length of teats or testes; annuli in dental cementum are believed to correspond to age in years; FEATURES (SIZE) - average weights for adult males was 14.1 kg (n=7, range 12.5- 15.9) and for females was 9.9 kg (n=12, 9.5-10.9); kits were 55% (males) and 65% (females) of average adult weight by early July (age 4 months), and were within the range of adults by mid-November at 8.5 months (males) and mid-February at 11.5 months (females); a male kit grew 4 mm/day in length and 74 g/day in weight from 12 May to 19 August; REPRODUCTION - based on observations of 6 collared adult females over a 5-year period, the "reproductive rate" (kits produced) was 0.69 kits/female/year--adding results for 2 subadults, neither of which produced young, that figure is 0.60 kits/female/year; 1 female averaged 1.25 kits/year over a 4-year period (3 years with kits) while the rate for another was 0.00 kits/year over 3 years of observation: none of 5 collared animals produced young in 1980, an apparently hard year; unsuccessful pregnancies and/or early losses of kits were suspected in a few cases; litter size averaged 1.80 kits for all litters and 1.75 kits for those observed after abandonment of the natal den (i.e., age 2 months and older); MORTALITY - no natural mortality was documented; no trapping and only minimal hunting occurs in the area, but one collared male was taken locally by a hunter and 2 males (1 a juvenile after dispersal) were killed outside the study

area; apparent trap injuries on the feet of 2 animals suggested that they had dispersed into the area from elsewhere; HOME RANGE - summer ranges for females averaged 94 km^2 (n=11 female years, 8 individuals: range 38-318 km^2) and yearly ranges were only slightly larger at 103 km^2 (n=10 f-years, 7 indiv., range 53- 232); average home ranges varied from year to year, and females with young had smaller summer ranges (70 km^2, n=3, 56-99) than those without (97 km^2, n=5, 68-178); at least one female made a long-distance excursion (2-day period in May); male summer ranges averaged 626 km^2 (n=4, range 488-898) and yearly ranges were 666 km^2 (n=4, 488-917); the summer and annual ranges for 3 juvenile males were smaller, averaging 49 and 51 km^2, respectively; it is speculated that the density and reproductive condition of females in an area are more important to male home range size than food or habitat; TERRITORIALITY - resident females maintained ranges exclusive of other females, except for female offspring in summer--in one case the range of an adult and her female yearling daughter overlapped extensively; one female made "frequent excursions" into the ranges of other females in winter 1980, probably because of "impending starvation"; male ranges overlapped those of females (usually 4-6 of them) and juvenile males, but data were inadequate to determine whether the ranges of males were mutually exclusive; scent-marking, mostly by urine deposits on protruding objects, was conspicuous (e.g., 40 deposits in 20 km of trail) and was done by both sexes; deposition of secretions from ventral and/or anal glands also occurred, by rubbing--and this appeared to be done with greater "excitement" than was the case for urine deposition; MOVEMENTS - the average distance between daily locations (ADDL) varied seasonally, yearly, and among individuals, and was shown to underestimate distances actually moved by 33% in monitored cases; ADDL in summer was 4.2 km for females and 12.3 for males (max. = 15.6 and 35.6 km, respectively); the average rate of travel for unpursued animals was 8.6 km/h for males and 4.6 km/h for females (max. = 10.6 and 8.0); ADDL for females with young was less than for those without, owing to the need to return to dens and/or rendezvous sites; adults (both sexes) moved only about 1 km/day when paired during the mating season; data indicated that males were much more active than females in summer, probably to monitor the several local females for breeding condition; DISPERSAL - dispersal of juveniles occurred during their first winter, but not all juveniles dispersed; one female was still in her natal area at 28 months (July); one juvenile male was last monitored on its natal range in mid-November, but dispersed between that date and the following March and was trapped 100 km to the south; other documented dispersals included a juvenile male that left between 9 and 11 March, after periodic forays (10 km) away from his mother in the previous 2-3 weeks, and was relocated 60 km south; an eartagged female, believed a yearling marked on the study area in October, was trapped 300 km south the following January; WEATHER EFFECTS - one apparently old female repeatedly intruded on other female ranges, was livetrapped several times in succession, was the only livetrapped animal to eat the bait, and killed and ate one trapped red fox and tried to obtain another, all in the severe winter of 1980--that year was characterized by reproductive failure of all 5 marked females the following spring; BEHAVIOR - females and young are in the natal den for a large proportion of time in March and April, but appear to vacate by early May--probably mostly because of snow melt; females appeared to leave dens to hunt mostly during the

mid-day hours--this pattern possibly related to ground squirrel activity at that time; females did not move young from dens when disturbed by human observers; after abandonment of the den, kits are periodically moved to a series of rendezvous sites, where the females leave them when they go foraging; by late June kits travel with their mothers, but may be found separate from them increasingly after August; interactions between mother and young occur throughout the first year, and sometimes longer (especially for female young); breeding behavior was observed (see Magoun and Valkenburg 1983); **FOOD HABITS** - most data are presented in Magoun (1987); caching behavior was conspicuous, with wolverines burying ptarmigan, ground squirrel, and caribou remains in summer, and with frequent evidence of digging out caches in winter; some of the caches utilized by wolverines were believed to have been made by other species, particularly red foxes (whose tracks wolverines regularly followed) and grizzly bears; berries and insects, used in summer in other areas, were uncommon and rarely used in this tundra study area; **DENNING** - detailed diagrams of the extensive snow tunnel systems dug and used as dens are presented; **HARVEST CHARACTERISTICS** - males dominated the harvest in northwestern Alaska, but most harvest was during the denning season (when females were frequently in dens and therefore less vulnerable) and was by shooting rather than trapping; it is suggested that because male ranges are larger, there are fewer of them therefore males are likely to remain transients (with greater vulnerability) longer than females; **MANAGEMENT CONSIDERATIONS** - the most important factor acting on wolverine populations in the area is thought to be food abundance, with particular reference to caribou whose distribution and abundance in the area varies from year to year; a conservative estimate of 821 animals (1 per 48 km^2) is calculated for the foothills region of GMU 26A (1 per 139 km^2 if the adjacent coastal plain area is included); based on known harvests and theoretical considerations of natality and survival observed during the study, it is concluded that the populations in the area were not being overexploited; a skull collection program to ascertain harvest age and sex ratios is recommended as a minimum (and efficient) harvest monitoring activity.

* Magoun, A.J. 1987. Summer and winter diets of wolverines, *Gulo gulo*, in arctic Alaska. Can. Field-Nat. 101:392-397.

A) 3; B) Alaska; C) Field and laboratory studies.
Life History - food, behavior, health.
Population Dynamics - natality.
Species Management - popreg.
Comments - The study was conducted north of the treeline, where no ungulate wintering occurs; the summer diet, as determined by direct observation of feeding behavior

(capturing, carrying, caching, or eating) among radio-collared animals consisted of arctic ground squirrels (19 of 48 observations, 39.6%), caribou (6, 12.5%), other small mammals (6, 12.5%), 1 observation each of marmot and Willow Ptarmigan (2.1%), and 15 unidentified (probably mostly small mammals and/or birds; of 82 scats collected along winter trails, the top 3 items by frequency of occurrence/percentage dry weight were ground squirrel (40/32), caribou (37/35), and other small mammals (lemmings, voles, shrews, 30/6), while birds and/or eggs (11/3) and unidentified food remains (13/3) also occurred; soil was a frequent and occasionally significant component of scats, particularly those from mid-winter, and was believed to be related to use of cached ground squirrels and/or live or dead individuals in hibernacula; a total of 186 wolverine "digs", with 110 of them into soil, were tabulated along about 80 km of winter trails; caribou and ground squirrels accounted for 92% (weight) of scats collected from natal den sites (representing food consumed primarily in March and April), but the percentages differed between years and between individual sites; it is concluded that wolverines are opportunistic in their food habits, their diet reflecting annual and seasonal changes in food availability; the approximate sequence of food availability and use on the study area was as follows: 1) ground squirrels dominated in the diet from late March through early May (when they first emerged from hibernation), 2) small mammals and birds/eggs increased in the diet in May and June as snow exposed the former and the latter commenced local breeding, 3) caribou migrated through and produced young (late May through June)--with some of all ages dying and/or killed by predators at that time and becoming available to wolverines, 4) ground squirrels increasing in vulnerability during emergence and dispersal of young (especially in August), 5) decreased food availability, October through March, with most ground squirrels apparently taken from caches and old caribou kills being used up; it appears that wolverines are able to derive some nourishment from scanty remains, including bone, but while they may be able to survive a lean winter they may not be able to reproduce the following spring--in one such year, 1979-80, all of 5 radio-collared females failed to produce young; one female, in winter 1981-82, left an established home range in apparent response to a food shortage.

Magoun, A.J., and P.S. Gipson. 1985. Ecology of wolverines in an arctic ecosystem.

Life history
Arctic Alaska

This paper is a concise summary of Magoun's three year study of wolverines in arctic Alaska ending in 1980. All of the information presented here is summarized in Magoun (1985).

* Magoun, A.J., and P. Valkenburg. 1983. Breeding behavior of free-ranging wolverines (*Gulo gulo*). Acta Zool. Fenn. 174:175-177.

A) 2; B) Alaska; C) Telemetry-aided field observations.
Life History - behavior.
Population Dynamics - natality.
Comments - Three pairs of breeding wolverines, both members known (radio-collared) in two cases and a known female with an unknown male in the third, were observed; breeding pairs were observed together for up to 2.3 days, and the relationship prior to copulation in two cases was characterized by agonistic behavior from the female in response to male advances; copulation dates were 5 and 11 June 1980 and 6 August 1979, the last date extending the known breeding period for the species; 1 female copulated twice in one day, and both bred in consecutive years, whether or not kits were produced in the previous year.

* Makridin, V.P. 1964. The distribution and biology of the wolverine in the far north. Zool. Zhumal 43:1688-1692.

A) 1; B) USSR; C) Field observations and laboratory examination of specimens, incidental to aerial predator control activities.
Description - features.
Life History - food, behavior.
Population Dynamics - poptrend.
Species Management - economics, interactions.
Comments - It is noted that despite their wide distribution and an abundance of food resources, wolverines are rare--found much less frequently than wolves "...even though no special extermination measures have been taken against them" and they have "...no natural enemies other than the wolf"; the yield in some of the more productive areas for the species is given as less than 1 pelt per 5000 km^2 during peak times; it is speculated that low population numbers may be due to reproductive factors, including late maturation (age 3?), alternate year or less frequent breeding, and possibly missed breeding because low densities make it difficult for the animals to find each other; the primary habitat for the species in the northern USSR is "forest tundra", and it is noted that when pursued by aircraft wolverines usually try to escape by hiding in the forest or burrowing into the snow; measurements and weights are given for 14 specimens (9M, 5F)--male weights ranged from 12.5-17.0 kg (mean 14.0) and comparable figures for females were 9.0- 10.4 (9.9); 13 of 16 stomachs examined contained reindeer and 5 contained ptarmigan--those are said to be the two most common species in the tundra and forest-tundra habitats in winter; in winter the wolverine "...confines its movements to reindeer pastures or areas where wild deer or elk congregate," and "...frequently follow wolves and pick over remnants of their prey"; wolverines account for considerable losses in the reindeer herding industry and are "the scourge of polar fox trappers", and the concluded statement notes that "...it is essential that bounties be offered for its extermination and that it be eradicated from most of the regions of the Far North."

McKay, R. 1991. Biological assessment and inventory plan for the wolverine (*Gulo gulo*) in the Uinta Mountains. Utah Natural Heritage Program and Utah Dept. of Natl. Resources, Salt Lake City. 58pp.

Bibliography and literature review
Utah

This document contains a summary of wolverine biology and management, including its habitat needs; a review of historical records, inquiries, and interviews to determine past sightings and locations of wolverines in Utah; an inventory plan, including a recommendation of procedures, and cost estimates; and an annotated bibliography.

Mead, E.M., and J.I Mead. 1989. Snake Creek Burial Cave and a review of the quaternary mustelids of the Great Basin. The Great Basin Naturalist 49:143-154.

Paleohistory and distribution
Nevada

ABSTRACT
Snake Creek Burial Cave (SCBC), east central Nevada, is a unique paleontological deposit. The cave is the first natural trap excavated in the Great Basin and one of the few localities describing a valley-bottom community. The recovery of extinct *Camelops* sp. (camel) and *Equus* spp. (horse), in addition to radiometric dates, indicate at least some of the deposits to be of late Pleistocene age. Eight mustelid species have been identified from SCBC, including three species not previously reported from the late Rancholabrean of the Great Basin: *Mustela nigripes* (black-footed ferret), *M. nivalis* (least weasel), and *Gulo gulo* (wolverine). A review of late Pleistocene deposits indicates that there are more species of mustelids recovered from Snake Creek Burial Cave than from any other locality in the Great Basin.

Mehrer, C.F. 1976. Gestation period in the wolverine, Gulo gulo). ** Journal of Mammalogy 56:752-757.

A 10 year old female mated with a male of unknown age and gave birth to one female and two male kits after 272 days gestation period at the Dakota Zoo in Bismarck, North Dakota. The kits were born completely covered with white fur, eyes closed, and teeth unerupted. Their average weight was 84 grams, average crown-rump length was 12.1 cm. Also mentioned was a birth at the Copenhagen Zoo which took place after a gestation period of 215 days.

Miller, G.C. 1980. Lynx and wolverine verification. Project ** Number SE-3-3. Colorado Division of Wildlife.

Wolverines have been reported to exist in 20 Colorado counties. Verification of wolverine presence has been made for only four counties: Summit, Clear Creek, Ouray, and the Montrose-Gunnison county line. Of 271 wolverine observations reported, and current field work, there is no "irrefutable evidence of a viable wolverine population" in Colorado. However, there is some circumstantial evidence that wolverines may exist in Colorado.

Colorado Department of Wildlife personnel utilized the following steps to reach their goal of wolverine verification in the state:

1. Review published and unpublished records of wolverine sightings, sign or specimens.

2. Requested information through a state wide request which utilizes slide presentations, "wanted" posters issued to trappers, taxidermists, outfitters, private individuals, personnel of appropriate state and federal agencies.

3. Rated the information obtained, and initiated follow-up telephone interviews.

4. Determined field study areas based on the geographical distribution of observation reports. Searches were made for tracks and trails using snowmobiles and skis. Baited hair traps were used to determine further the presence of wolverine on the study areas. No wolverine fur was found in the hair traps.

This paper reports some interesting trends derived from the observation reports. First, wolverines were observed at lower elevations during the winter. These winter reports were usually associated with oakbrush, sagebrush, or fields at the lower montane ecotone. Additionally, these locations are closely associated with ungulate winter ranges. The distribution of winter reports further suggests that wolverines may use south facing slopes more often.

Myhre, R. and S. Myrberget. 1975. Diet of wolverines (Gulo gulo) ** in Norway. Journal of Mammalogy 56:752-757.

Examination of seventy-six stomachs revealed the following percent occurrence of food in the wolverines' diet: 81.6% reindeer (Rangifer taranadus), 7.9% moose (Alces), 3.9% red fox (Vulpes vulpes), 3.9% hare (Lepus timidus), 2.6% roe deer(Capreolus capreolus), 14.5% small mammals, 6.6% birds. Reindeer appears to be the most important winter food. Myhre and Myrberget suggest that kits eat solid food at the age of 7-8 weeks and that wolverine and lynx can coexist in the Norwegian mountains because of different hunting techniques and usage of prey.

Myrberget, S. 1968. The breeding den of the wolverine, Gulo gulo. ** Fauna 21:108-115. (In Norwegian with an English summary).

The English summary can be easily located in Biological Abstracts. Hunters provided the description of 28 wolverine dens from Norway. Elevation ranged from 200 to 1500 meters above sea level, but most dens were found between 500 and 1000 m. Fifteen out of 25 dens were found in open mountain tundra. Eight of these dens were at treeline or in higher-elevation birch forests. Two were in mixed birch and pine forests. Fifteen out of 20 were on southern aspects. The dens were most often found in 3 to 5 meters of snow, next to small cliff faces. One was under a 3 by 5 meter stone. Most dens (N=20) had one entrance, the diameters of which were 30 to 40 centimeters. Dens generally feature 1 to 2 main tunnels from 5 to 60 meters long, most being 12 to 30 meters long. Food and excrements were found in "definite" locations. The pits of ten dens were mostly lined with branches. Snow and no cover were also found. Female wolverines transplanted their young into secondary dens when disturbed by humans. These dens were usually less developed. Wolverines were observed to leave their dens permanently around mid May.

* Nead, D.M., J.C. Halfpenny, and S. Bissell. 1984. The status of wolverines in Colorado. Northwest Sci. 58:286-289.

A) 0; B) Colorado; C) Literature review, compilation of solicited sight records, and attempts to confirm reports in the field.
Description - distribution.
Population Dynamics - poptrend.
Comments - Evidence gathered in recent years indicate that wolverines still exist in Colorado (at or near the southern limits of their continental distribution), but it is not certain that there is a "viable population" in the state; wolverines have been protected by law in Colorado since 1965, and has been classified as an endangered species in the state since 1973.

* Newby, F.E., and J.J. McDougal. 1964. Range extension of the wolverine in Montana. J. Mammal. 45:485-487.

A) 1; B) Montana; C) Compilation of specimen and sight records.
Description - distribution.
Population Dynamics - poptrend.
Comments - A total of 17 new records (1957-1962), 10 involving specimens, indicate that the wolverine has continued to expand its range in Montana, mainly into the southwestern portion of the state, after near extinction in about 1920, and a gradual reappearance (mostly in the northwest) beginning in about 1940; many of the recent specimens were males, suggesting that they are the pioneering sex; females with young, indicating successful reproduction, have been reported more frequently in the northwest (e.g., Glacier National Park), where recolonization of Montana is believed to have begun.

* Newby, F.E., and P.L. Wright. 1955. Distribution and status of the wolverine in Montana. J. Mammal. 36:248-253.

A) 1; B) Montana; C) Analysis of sighting and capture records.
Description - distribution.
Population Dynamics - poptrend.
Species Management - refuges.
Other Topics - history.
Comments - The Montana wolverine population was believed to have declined almost to extinction by the late 1920's, although it is acknowledged that there is little information on abundance for earlier years; records since the late 1930's suggest that the species has again increased, although it is suspected that dispersal from Canada and protected wilderness in Glacier National Park made such an increase possible; it is speculated that there were also indirect benefits to wolverine from closed or limited marten trapping seasons and from reduced fur prices for both marten and lynx in the 1940's and 1950's-- thus reducing trapping activity and incidental catch of wolverines; records for the early 1950's include individuals in isolated ranges away from the "normal" forested mountains habitat of western Montana, and observation of at least one family group and several pairs.

* Patterson, J.R., and E.L. Bowhay. 1968. Four recent records of wolverines in Washington. Murrelet 49:12-13.

A) 1; B) Washington; C) Compilation of specimen and sight records.
Description - features, distribution.
Comments - Following a hiatus of wolverine records anywhere in the state for over 20 years, 3 animals were killed and another seen in central (1) and southern (3) counties, April 1963, November 1964, and March 1965; all 3 of the kills involved adult males--2 that were weighed were 28 and 29 lbs (12.7 and 13.2 kg), respectively; reference is also made to an unpublished report of an adult male killed in the Cascade Mountains of Oregon in September 1965--the first authentic record for that state since 1912.

* Pengelley, L.W. 1951. Recent records of wolverines in Idaho. J. Mammal. 32:224-225.

A) 1; B) Idaho; C) Compilation of specimen and sight records.
Description - features, distribution.
Comments - An adult male, captured in October 1949 and weighing 22 lbs (10.0 kg) after 2-3 days in a trap, apparently constitutes the first authentic specimen record for the state; a few historical anecdotes and two recent (1948 and 1949) sight records are also given; all but one of the records (1926) are from the north (panhandle) area.

* Pulliainen, E. 1963. Occurrence and habits of the wolverine (*Gulo gulo*) in Finland. Suomen Riista 16:109-119.

Not seen, but findings have been cited in many papers; identified as a "very useful" paper by Dagg and Campbell (1974a), with keywords indicating coverage of distribution, food, numbers, reproduction, sex ratio, and economics.

* Pulliainen, E. 1968. Breeding biology of the wolverine (*Gulo gulo* L.) in Finland. Ann. Zool. Fenn. 5:338-344.

A) 2; B) Finland; C) Interviews with "wolverine (bounty) hunters".
Life History - denning.
Population Dynamics - natality.
Comments - Data were gathered from 31 natal dens; 25 of the dens (81%) were situated in rocky (fell) habitats--10 (32%) in deep ravines, 8 (26%) at timberline on gentle slopes, and 7 (23%) on similar terrain in subalpine or alpine terrain; the remaining 6 dens (19%) were in spruce and pine peat bogs; all but one were under deep snow (1-3 m), at the ends of tunnels up to 30 m in length, and it is postulated that the snow cover is an important component of natal dens primarily because of its insulative value--the single exception among the 31 dens observed was a den under "spruce brush" at the base of a spruce; in most cases the nest itself was at ground level in a snow chamber, although fallen trees often formed the roof of the chamber where they were present; none of 17 dens in northern Lapland were associated with trees (apparently because trees were generally not available), but 8 of 14 in the taiga habitats of northeastern Lapland used tree structures in some way; for 30 ostensibly complete litters, average litter size was 2.4, with the following frequencies: 1 cub - 4 (13%), 2 cubs - 11 (37%), 3 cubs - 13 (43%), and 4 cubs - 2 (7%); the mean for 161 litters, adding results for other fennoscandian countries, was 2.5, with the following frequencies: 1 cub - 5 (3%), 2 cubs - 81 (50%), 3 cubs - 66 (41%), 4 cubs - 9 (6%); an *in utero* litter of 5 fetuses, near term (15 March 1956), is reported; the sex ratio among 39 sexed cubs was 23 males and 16 females (59:41); the parturition period in Finland lasts about 2 months (late January through late March; males were believed to have visited dens in a few instances, but their parental role (if any) was not evident; female wolverines brought food, mostly carrion, from up to 20 km away and daily movements of 30-40 km away from dens were reported; food items were often stored near the den--in one case 2 reindeer, 39 whole ptarmigan, 32 ptarmigan wings, and the head of a hare (the ptarmigan apparently "stolen" from hunters' traps); one female reportedly killed 12 female reindeer in 4 nights.

* Quick, H.F. 1953b. Wolverine, fisher, and marten studies in a wilderness region. Trans. N. Amer. Wildl. Conf. 18: 513-532.

A) 2; B) British Columbia; C) Field observations and collection of specimens on some northern traplines.
Description - distribution.
Habitat Characteristics - cover.
Life History - movements, behavior.
Population Dynamics - poptrend, popcomp.
Species Management - economics, harvest.
Comments - Based on fur sales data, it is concluded that the Fort Nelson study area may be "a center of wolverine population in western Canada"; acknowledging that yield is related to effort, it is believed that trapping intensity is more directly related to population density in this species than in most others because of the animal's destructive nature and because "...market value does not materially affect trapping intensity"; nevertheless, it is noted that fur sales data are minimal because wolverine pelts are often kept by the trapper and/or sold privately at other than normal outlets; of 44 wolverines known to have been trapped in the study area in 1947 and 1948, only 27 (61%) were killed--the remaining 17 escaped, leaving 1 or more toes in the trap and thereby potentially providing for some consideration of total numbers on a "mark and recapture" basis; observation of tracks along trapline trails and reports from trappers indicated that wolverine abundance was about the same in all of three different habitat "zones" in the study area (muskeg, foothill, and mountain--physiographic subdivisions within the general "Taiga Biome"); the density estimate for the 51 200 km^2 study area was about 1 animal per 207 km^2, for a projected total local population of about 250 animals; recorded harvests for the two study years were 15 and 12 (6.0 and 4.8 per cent of the projected population, respectively); of the 27 wolverines known to have been killed in the study area in the two years, 15 were collected (9 males and 6 females)-- male weights ranged up to 25 lbs (11.3 kg), but females were listed at only 12 lbs (5.4 kg); observations indicated that the wolverine is more of a scavenger than a killer, regularly following "...skillful hunters like lynx, wolf and man"; an account of trapline depredations indicates that wolverines caused less damage and loss of furs than wolves in the study years, and probably less than shrews in all years, although there were regular reports of damage to property such as cabins, panniers, dog harnesses and human food caches; the fur value of wolverines taken in the study area amounted to less than 1% of the total fur revenue in the area overall; it is concluded that the species is unimportant in the fur trade owing to its characteristically low density occurrence, relatively low value per pelt, and the fact that the value of its damage may often exceed the revenues from pelt sales.

* Rausch, R.A., and A.M. Pearson. 1972. Notes on the wolverine in Alaska and the Yukon Territory. J. Wildl. Manage. 36:249-268.

A) 3; B) Alaska, Yukon Territory; C) Laboratory analysis of specimens and some incidental field observations.
Description - features.
Life History - food, health, denning.
Population Dynamics - natality, popcomp.
Species Management - age/tech, repro, harvest, harv/strategy.
Habitat Management - other/impacts, hab/strategy.
Comments - Note: There are numerous mathematical errors in this paper, especially in Table 5, and the reader is cautioned to check reported numbers before using them--most of the data reported in the present review have been checked and/or recalculated, as appropriate, although some errors may still remain; FEATURES (SIZE) - the whole weights of six males averaged 32 lbs., with a range of 29-37 (14.5 kg, 13.2-16.8), while the weights of two females were 21 and 22 lbs (9.5 and 10.0 kg); the projected live weight for one Alaskan male, examined as a skinned carcass, was 42.5 lbs (19.3 kg)--the heaviest wolverine reported; in a sample of 99 whole wolverines from the Yukon, the weights (means and ranges), and sample sizes by age class were as follows:

Males
adults - 31.2, 26.2-36.3 lbs (14.2, 11.9-16.5 kg), n=52
kits - 29.1, 20.7-37.2 lbs (13.2, 9.4-16.9 kg), n=19

Females
adults - 20.7, 18.4-23.7 lbs (9.4, 8.3-10.8 kg), n=21
kits - 20.1, 18.0-22.6 lbs (9.1, 8.2-10.3 kg), n= 7

REPRODUCTION - based on cementum age determinations, none of 109 female wolverines in age class 0 (0-15 months old) were pregnant, while 20 of 40 (50%) in age class 1 (16-28 months) and 90 of 98 (92%) in age classes 2-13 (29 months plus) were; breeding apparently occurs primarily in May through July, implantation in December through March, and most parturition in February and March; males were sexually inactive in late fall and winter, but testis size increased and spermatogenesis began to occur in late winter, peaking in about late May and June; as with females, some (but not all) males were sexually mature by the breeding season of their second year; *in utero* litter sizes of 1-6 were documented, with an average of 3.5 per litter (n=54); among the sample years (1961-68), mean litter sizes of less than 3 were recorded in two (1962 - 2.6, n=5; 1965 - 2.7, n=7), while in 1966 a sample of 5 included four litters of 5 and one of 6 (mean=5.2); DENNING - of three natal dens observed in Alaska, two were above timberline in snow-filled ravines and one was in an abandoned beaver house; well-used moose carcasses were present near the two ravine sites; AGE DETERMINATION AND HARVEST COMPOSITION - young wolverines grow and develop quickly, reaching adult size by November or December of the first year (age 9-11 months); rapid development of skeletal

features reduces options for distinguishing between young and adults--dental cementum is considered the most reliable (although known-aged specimens are still required); males outnumbered females in the trapped samples, but only by 128:100 among kits (age class 0) as compared to 200:100, 450:100, and 178:100 in age classes 1-3, respectively--the ratio among older animals (age classes 5- 12 combined) was 100:100; the even sex ratio among kits is speculated to result from the fact that they had not yet established territories and the sexes were still equally trappable at that age, while the preponderance of young males in the age 1-3 classes is due to greater mobility of males and the even ratio among older animals "...may reflect a reduction of males through exploitation"; **CONDITION** - Kidney fat indices indicated that animals were in the best physiological condition in spring (March-April) and poorest in summer (May-September)--it is speculated that spring is the period of highest food availability for wolverines, especially in terms of ungulate carrion, and that the reproductive cycle is timed to take advantage of that; **FOOD HABITS** - in 94 stomachs containing food and/or trap debris, the top three food items by frequency of occurrence were moose (27 occurrences = 29%), snowshoe hare (23, 24%), and caribou (17, 18%)--other foods included microtines (9%), unident. flesh (6%), bird (3%), fish (3%), beaver (2%), and traces of lynx--the large mammals were believed to have been taken mostly as carrion; it is noted that the wolverine's summer food habits are not well known, but that microtines, ground squirrels, and marmots are taken, and that berries may be heavily used--the stomach of a Yukon specimen shot in September contained 190 g of blueberries; two instances of internal damage from porcupine quills are reported; **MANAGEMENT** - the wolverine was subject to bounty in Alaska, 1953-1968, but is now classified as a furbearer and big game species; Alaskan harvests have fluctuated considerably over the years (from 300 or fewer to almost 700 animals in the 1950's and 1960's)--the variation is probably mostly related to the general level of trapping activity (e.g. high harvests in the 1960's when lynx were abundant and bringing good prices); management actions believed favorable to wolverines in Alaska, in addition to removal of the bounty, have been outlawing of aerial hunting for the species and termination/reduction of poison baiting aimed at wolves; in regard to poisoning, it is noted that wolverines, "...because of their proclivity for carrion, were particularly susceptible to those nonselective control techniques"; the wolverine is classified as predator and furbearer in the Yukon, with the annual kill attributable to all sources including predator control baiting averaging about 150 animals, but apparently decreasing due both to recently reduced use of strychnine and decreased trapping activity; habitat changes are not considered a threat in Alaska and the Yukon, but garbage and firearm control at remote exploration camps is recommended to minimize detrimental effects on local wolverines.

Robart, G. 1982. Wolverine, fisher, marten sightings in Oregon
** 1973 - 1982. Supplementary Report. Oregon Department of Fish and Wildlife. Central Region Administrative Report No. 82-4.

This paper summarizes the wolverine sightings reported to the Oregon Department of Wildlife from 1973-1982. Twenty-nine sightings were reported. Biologists believe that wolverines persist in Oregon based on the number and locations (mostly on the summit of the Cascade Range, above 5000 feet) that wolverines persist in Oregon.

Roughton, R.D. and M.W. Sweeny. 1982. Refinements in scent-
** station methodology for assessing trends in carnivore populations. Journal of Wildlife Management 46(1):217-229.

This paper provides the methodology for using scent stations to attract carnivores. Each station is a circle of sifted earth with a saturated plastic disc filled with odor attractant. The stations should be checked daily for tracks. Recommendations: 1) survey lines of 10 stations each should be left for one night. New lines should be established daily to maximize distribution, such that the chance for repeated visits by the same individual is decreased. 2) Each station should be flat, devoid of litter, rocks, etc. The tracking surface should be made of sifted soil. Sand should be avoided as a tracking medium. 3) Timing is important, avoiding hunting seasons because of increased traffic on unimproved roads, and adverse weather conditions. The best time is when juveniles are dispersing. 4) Intervals between stations should be scaled to the mobility of species of interest, size of study area, and available road length. 5) Intervals between lines should be scaled to the mobility of the predator, large enough to minimize the chance of 1 individual visiting more than once per night.

Recommendations for attractant: 1) use the best scent to attract the species of interest. 2) FAS-fatty acid scent, is good for canids, and is recommended as standard comparison for other carnivores. 3) It is good to use same scent if can get enough for study. 4) Saturated plastic disc recommended as a low cost alternative for presenting scent in uniform quantity, rather than capsule form.

Computer analysis- Fisher Randomization Test is good for this type of data.

Schempf, P.F., and M. White. 1977. Status of 6 furbearer
* * populations in the mountains of northern California. USDA Forest Service. California Region. 51pp.

Wolverines used habitat types consisting of Douglas-fir (Pseudotsuga menziesii), mixed conifers, and lodgepole pine (Pinus contorta). The lowest elevation record for wolverines in California is 400 meters.

Singer, F.J. 1991. Some predictions concerning a wolf recovery into Yellowstone National Park: How wolf recovery may affect park visitors, ungulates, and other predators.

Predator interaction
Yellowstone National Park

Though several accounts of wolves killing wolverines exist, wolverines generally escape by climbing trees. As wolverines and wolves co-exist over a great part of their range, wolverines are not expected to be impacted if wolves recover in Yellowstone.

Telfer, E.S. and J.P. Kelsall. 1984. Adaptation of some large North American mammals for survival in snow. Ecol. 65:1828-1834.

Adaptation
General

ABSTRACT
Chest heights, foot loading, and behavior of moose (*Alces alces*), caribou (*Rangifer tarandus*), wapiti (*Cervus canadensis*), white-tailed deer (*Odocoileus virgineanus*), Dall sheep (*Ovis dalli*), bighorn sheep (*Ovis canadensis*), pronghorn antelope (*Antilocapra americana*), and bison (*Bison bison*) were used to calculate indices of snow-coping ability for each species. When species were grouped into regional faunas, those with higher indices occurred in more snowy regions. Within local area, a variety of species can survive in winter by living and feeding in different habitats defined on the basis of snow conditions. Bison, deer,and wapiti have considerable sexual dimorphism in chest height and foot loading. These differences between the sexes have potential value for individual survival in snow by permitting use of food resources over a greater

proportion of the species'home range. Wolves (*Canis lupus*), coyotes (*Canis latrans*), and wolverines (*Gulo luscus*) showed similar levels of morphological adaptation to snow, higher than all but two of the ungulates studied (caribou and moose); predation appears to have been a factor influencing evolution of ungulate behavior in snow.

⁎ Van Zyll de Jong, C.G. 1975. The distribution and abundance of the wolverine (*Gulo gulo*) in Canada. Can. Field-Nat. 89:431-437.

A) 2; B) Canada; C) Literature review.
Description - distribution.
Population Dynamics - poptrend.
Species Management - harvest.
Comments - The wolverine's status in Canada is summarized from available fur harvest and anecdotal information; the species is believed to have been less abundant in the east than in the west in pristine times, and has become "quite rare and restricted in distribution" east of the prairies--annual harvests in each of Ontario and Quebec (including Labrador) apparently has not exceeded 25 animals since the early 1920's and has been less than half that in all years since; in Manitoba, single-year harvests of over 150 are indicated for a few years in the early 1920's, but have remained at 25-50 thereafter--the occupied range has shrunk to the north, with the only known "center of abundance" occurring in the northwest corner; harvests up to 100 were reported for Saskatchewan in the early 1920's, but have been less than 25 in all years since, and the species' range in the province is apparently restricted to the extreme north; occurrence in Alberta is mainly in the north and in mountains along its western border--there were harvests of over 200 (up to about 350) in the 1920's, but the take in most years between 1930 and 1965 was less than 25--a slight trend to increase is evident since 1965, with some harvests in the 50-100 range; there has been no known change in distribution in British Columbia, and changes in abundance (as measured by pelt production) have been less there than in any of the other provinces--annual harvests of 200-300 were common from the 1920's through 1940's, fell off to an average of about 150 through the 1950's and early 1960's, but have shown a dramatic increase trend (to 400 plus) thereafter; in the Yukon, the highest recorded harvests were in the early 1930's, with at least 4 years in the 500-600 range, although most years before and since have been 200-300--no historic change in distribution is indicated, and the harvest trend in recent years (1970's) appears to be upward; occasional yearly harvests of 200- 300 are shown for the Northwest Territories in the 1920's and 1930's, but except for peaks of about 150 in the late 1930's and several years in the late 1950's, most years since the 1930's have produced 50-100 pelts--the distribution in NWT has apparently been maintained, but no trend to increasing numbers (as reflected in harvests) is apparent; it is noted that at the time of writing, there had been "...virtually no field studies on this continent", but the animal's

scavenging life style is apparent and that observed changes in Canadian distribution and abundance since the early part of this century are believed related mostly to human predation, changes in ungulate populations (especially caribou), and possibly wolf control.

* Whitman, J.S., W.B. Ballard, and C.L. Gardner. 1986. Home range and habitat use by wolverines in southcentral Alaska. J. Wildl. Manage. 50:460-462.

A) 2; B) Alaska; C) Field (telemetry) studies, 1980-83.
Habitat Characteristics - cover.
Life History - hmrange, movements.
Comments - Adequate data for home range considerations were obtained for 7 animals (4M,3F); males had significantly larger home ranges (535 km^2) than females (105 km^2), although all females had kits during most of the monitoring period and were therefore probably more sedentary than other females might have been; summer and winter ranges were similar in size, and overlapping--the animals tending to expand the overall annual range by using different areas in the two seasons; animals of both sexes moved to high elevation for summer, where ground squirrels, other small mammals and ground-nesting birds are plentiful, and in winter moved to lower elevations where ungulates dying from starvation and wolf predation were available; in summer, forest habitat types were avoided and other types (shrub, tundra, rock-ice) were used according to their availability; in winter, tundra was avoided and the other types used according to their availability.

Wilson, D.E. 1983. Wolverine. IN: Chapman, J.A. and G.S.
** Feldhamer, editors. Wild mammals of North America, biology, management, and economics. Johns Hopkins University Press. Baltimore.
p. 644-652.

This chapter provides information on distribution, physical description, physiology, reproduction, ecology, food habits, mortality, age determination, economic status, and current management and needs.

Winn, D.S. 1976. Relationships between terrestrial vertebrate
** fauna and selected coniferous forest habitat types on the north slope of the Uinta mountains. PhD dissertation. Utah State University. Logan.

This dissertation discusses the methods used to determine the relationships between some animal species and the forest communities. Winn used 3 scent posts, spaced 100 meters apart. The posts were oriented to each other in shape of an equilateral triangle. In each phase of the vegetative community type, as designated by Winn, 2 scent posts sites were surveyed for tracks, animals, or other sign during each sampling effort. Each site was surveyed twice every 24 hours, over a period of 4 consecutive nights. Thus, scent post stations were sampled 16 time per community phase. Additionally, two clearcuts were surveyed for 5 consecutive nights with 9 scent posts placed at 0.5 kilometer intervals across a 4 kilometer route. All stations were surveyed on the same mid-week days to reduce any bias encountered from weather and recreation.

Pellet and midden counts were made to assess the relative stability of snowshoe hare and red squirrel densities.

No wolverines visited the scent stations.

* Woods, G.T. 1944. Longevity of captive wolverines. Amer. Midland Nat. 31:505.

A) 1; B) General; C) Correspondence with various zoological parks.
Population Dynamics - popcomp.
Comments - Of 45 captive wolverines for which information was received, and which survived at least 6 months, the average length of life was about 5.5 years; the maxima recorded were for 4 animals listed as "close to 16 years old" and one other at 15 years.

* Wright, P.L., and R.L. Rausch. 1955. Reproduction in the wolverine, *Gulo gulo*. J. Mammal. 36:346-355.

A) 2; B) Alaska; C) Laboratory examination of 33 trapped specimens.
Population Dynamics - natality.
Species Management - age/tech.
Comments - These studies confirmed that delayed implantation occurs in the wolverine--adult females taken in October through mid-January showed unimplanted blastocysts in their uteri and inactive corpora lutea in their ovaries; embryos were found in 2 females, taken 20 January and 2 February, and 2 females taken in April were lactating; implied "litter" sizes were: blastocysts - 2,4,4; embryos - 3,4; placental scars - 3,3; it was concluded that breeding probably occurs in mid-summer, implantation in January, and birth

in late March or early April; the testes of males were largely inactive in winter, when the specimens were collected--only 1 of 22 (taken in early April) showed signs of full sexual activity; the evidence indicated that sexual maturity was reached by both sexes in the second year; the skull matures rapidly, although the extent of the sagittal crest remains a method of distinguishing between adults and juveniles.

* Yocom, C.F. 1973. Wolverine records in the Pacific coastal states and new records for northern California. Calif. Fish Game 59:207-209.

A) 0; B) California; C) Literature review and compilation of incidental sight records.
Description - distribution.
Population Dynamics - poptrend.
Comments - A total of 12 sight records between 1958 and 1970, and recent literature reports of animals in Washington and Oregon, are taken to indicate that the species "...may be increasing in abundance in these portions of their ranges since the late 1950's"; in particular, it is believed that wolverines are becoming established in the mountainous areas of northwestern California.

* Yocom, C.F. 1974. Recent wolverine records in Washington and Oregon. Murrelet 55:15-18.

A) 1; B) Washington, Oregon; C) Compilation of specimen and sight records.

S E L E C T E D R E P R I N T S

Copies of the following literature on wolverine appear here in their entirety (except those marked with [*], which appear here in part):

Banci and Harestad 1988

Banci and Harestad 1990

* Deems and Pursely 1983

Gardner et al. 1986

Groves 1988

Hash 1987

Hash and Hornocker 1980

Hoak et al. 1982

* Jackson 1961

Magoun and Gipson 1985

Newby and McDougal 1964

Newby and Wright 1955

* Obbard et al. 1987

Rausch and Pearson 1972

Whitman et al. 1986

Wright and Rausch 1955

Ann. Zool. Fennici 25:265–270. 1988

Reproduction and natality of wolverine (*Gulo gulo*) in Yukon

Vivian Banci & Alton Harestad

Banci, V. & Harestad, A. 1988: Reproduction and natality of wolverine (*Gulo gulo*) in Yukon. — Ann. Zool. Fennici 25:265–270.

In Yukon, female wolverine did not breed as young of year and only 7% of subadults were pregnant. Of the adult females, 53% of 2+ year-olds were pregnant or post-partum and between 62% and 92% of 3+ year-old and older wolverine were pregnant or post-partum. The mean *in utero* litter size was 3.2 ± 0.8 *SD* (n = 22). Natality increased with age, ranging from a mean of 2.8 to 3.4 fetuses per adult female. Pregnant females were caught in all months of the trapping season (1 November to 31 March) indicating implantation occurred at least as early as November. Males were sexually mature by 2+ years of age. Bacula length and weight should not be used as criteria of age without other evidence.

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1. Introduction

Wolverine, like many of the Mustelidae, have delayed implantation (Wright & Rausch 1955). Breeding is thought to occur between April and October but primarily in mid-summer (Wright & Rausch 1955). Wolverine have bred in captivity during May (Mehrer 1976) and July (Mohr 1938), and in the wild during June (Krott & Gardner 1985) and August (Magoun & Valkenburg 1983). Implantation of blastocysts occurs from December through March (Rausch & Pearson 1972). Birth of 2 to 4 kits occurs in late winter and spring (Wright and Rausch 1955, Rausch & Pearson 1972, Liskop et al. 1981).

Knowledge of reproduction is central to population dynamics of wolverine and essential for determining timing and rates of harvest in Yukon. Our objectives were: to determine when proestrus, implantation, and parturition ocurs; to determine age of sexual maturity for males and females; and to estimate age-specific natality. Age-related characteristics of the baculum have been used to distinguish young from adult mustelids (King 1980). Wolverine are difficult to age (Banci 1982) and our large sample presented an opportunity to investigate the utility of bacula for aging male wolverine.

2. Methods

Wolverine carcasses were obtained from trappers in Yukon over 3 winters, 1982–83 to 1984–85. The trapping season in Yukon extends from 1 November to 31 March and our description of reproduction is limited to this period. Two upper premolars were processed for each carcass. If upper premolars were unavailable, lower premolars or canines were used. Teeth were decalcified, sectioned at 10 microns using a freezing microtome, and stained with Tolulene Blue. Ages were determined from annuli and age class was estimated using skull characteristics. Because young wolverine are born during late winter through summer, age at capture of young of year in winter will be about 0.5 years. Consequently, ages are presented as 0+, 1+, 2+, and so on. We classed age 0+ as "young of year", 1+ as "subadult" and 2+ and older as "adult".

Usable specimens consisted of 168 female reproductive tracts, 199 testes pairs, and 194 bacula. Difficulties in aging reduced these sample sizes for some analyses. For females, reproductive tracts were removed and frozen whole. Tracts were thawed and ovaries sliced longitudinally in 1 mm secuons under a dissecting microscope. Corpora lutea were counted and the presence of developing follicles recorded. Corpora lutea regress rapidly after parturition (Rausch & Pearson 1972) and are an exact count of the number of ova shed for the most recent litter.

General characteristics of uteri were noted (not bred, thickened walls, flaccid). An attempt was made to flush uterine horns for blastocysts (Hamilton & Cook 1955) but few blastocysts were recovered and the technique was abandoned. Flushing does not appear to be a reliable technique for the recovery of

Table 1. Reproduction of female wolverine from Yukon 1982–1985. For adult females (2+ or older) corpora lutea were determined from pregnant or post-partum wolverine.

Age	*n*	% pregnant or post partum	Corpora lutea *n*	Corpora lutea mean±*SD*	Estimated* fetuses
0+	62	0.0	62	0.0±0.0	0.0
1+	27	7.4	27	0.2±0.8	0.2
2+	30	53.3	15	3.1±0.8	2.8
3+	13	92.3	10	3.6±0.7	3.1
4+	13	92.3	10	4.1±1.0	3.4
5+	7	85.7	6	4.2±0.8	3.4
6+–11+	8	62.5	5	4.4±1.1	3.4

*Linear interpolation using known relationship between number of corpora lutea and mean number of fetuses for females having in utero litters.

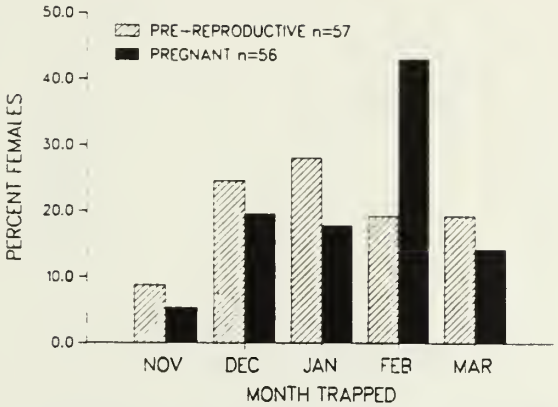

Fig. 1. Pre-reproductive and pregnant wolverine trapped November to March, Yukon 1982–1985.

blastocysts because loss rate is high (Rausch & Pearson 1972, Liskop et al. 1981). In addition, carcasses were in varying stages of decomposition and the condition of the blastocysts was questionable. Uterine horns were slit longitudinally and examined for placental scars. Regression of placental scars is relatively rapid (Rausch & Pearson 1972), therefore counts are not biased by scars from previous litters. If females were macroscopically pregnant, fetuses were removed, weighed and crown-rump length measured. Females were classified as: non-reproductive (no corpora lutea, no developing follicles, no placental scars); pre-reproductive (developing follicles present in ovaries); pregnant (corpora lutea, implantation sites or fetuses present); post-partum (degenerating corpora lutea, fading scars, flaccid reproductive tract).

The relationship between mean number of fetuses and number of corpora lutea was examined for females having macroscopic embryos. Mean number of corpora lutea was calculated for each age class of females. Number of fetuses was estimated by linear interpolation between 2 data points of the known relationship between corpora lutea and fetuses. Mean numbers of corpora lutea, scars and fetuses were compared using t-tests.

Paired testes and epididymides were weighed. If only one testis was present, the weight of the pair was estimated by doubling the weight of the single testis. Carcasses were subject to varying degrees of dessication. Testes, being externally situated, were especially susceptible to drying. Because dessication was not consistent, weights were standardized by soaking testes in water for 24 hours. Bacula were stripped of flesh, cleaned by dermestid beetles and weighed. Maximum length was measured using dial calipers. Atypical bacula, those broken and rehealed in bent positions, were omitted. Oneway ANOVA to test for significance followed by multiple comparisons using Fisher's Modified Least Significant Difference were used to compare testes weights, bacula weight and bacula length among age classes. ANOVA was used to examine variation in mean weights of testes by age class and time of year. Means ± 1 standard deviation are reported.

3. Results

3.1. Females

Young of year females were either non-reproductive (21 of 62) or pre-reproductive (41 of 62) and 7% of subadults (2 of 27) were pregnant. The percent of females pregnant or post-partum was 73% (58 of 79) but varied by age (Table 1). Pregnant females were caught throughout the trapping season (Fig. 1), indicating implantation occurred at least as early as November. The variability of fetus crown-rump length (Fig. 2) suggests an extended period of implantation and subsequently, parturition. A female caught on 3 March was near term: the fully furred fetuses (n = 4) had a mean weight of 107.7 g and mean crown-rump length of 112.5 mm. In contrast, fetuses (n = 4) of a female trapped on 15 March had mean weights of 7.1 g and a mean crown-rump length of 53.0 mm. Of post-partum females (n = 7), 1 was captured in January and 5 in February. One post-partum female captured on 8 November had placental scars but no corpora lutea, indicating either a late birth or that absorbtion of embryos had occurred. Developing follicles as well as regressing corpora lutea were present in ovaries of all post-partum females.

Mean number of corpora lutea increased with age to a maximum of 4.4 ± 1.1 (Table 1). The smallest number of corpora lutea for pregnant females was 2. For 23 females with macroscopic embryos, mean number of corpora lutea (3.9 ± 1.0) overestimates

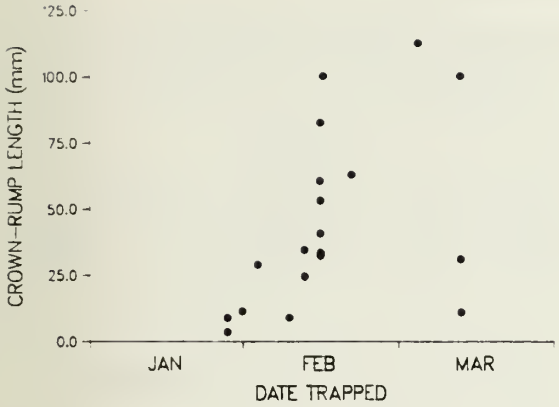

Fig. 2. Mean crown-rump length for *in utero* litters of wolverine trapped January to March, Yukon 1982–1985.

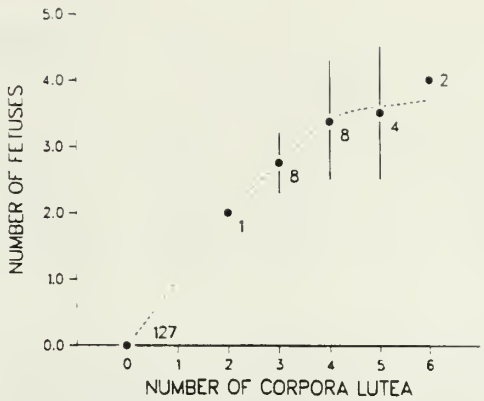

Fig. 3. Mean number of wolverine fetuses observed and number of corpora lutea, Yukon 1982–1985. Standard deviations and sample sizes are indicated.

mean number of fetuses observed (3.2 ± 0.8) (paired t_{22} = 3.87, P < 0.01). However, mean number of placental scars (3.3 ± 1.2, n = 18) did not differ from mean number of fetuses, (t_{40} = 0.36, P > 0.70). Neither counts of placental scars nor fetuses take into account embryos that are absorbed or young that die after birth. Of 19 litters having measurable fetuses, 1 fetus from a litter of 3 and 1 from a litter of 4 were beginning to disintegrate in the uterus.

For 23 females with macroscopic embryos, the number of corpora lutea is related to mean nmber of fetuses (Fig. 3). Using this relationship and mean counts of corpora lutea, number of fetuses was estimated for females of each age class (Table 1). The following assumptions were made in these calculations: a 1:1 relationship for $n \leq 2$ corpora lutea and fetuses; because only a small proportion of subadults reproduce, the estimated number of fetuses for this age class is the observed proportion; because the potential number of young mature females is capable of producing is independent of whether or not she becomes pregnant, mean corpora lutea counts include only adult females which were pregnant or post-partum.

3.2. Males

Oneway ANOVA indicated mean weights of testes differed among age classes of wolverine ($F_{2,196}$ = 44.96, P < 0.01). However, mean testes weights of subadults did not differ from young of year (P > 0.05)

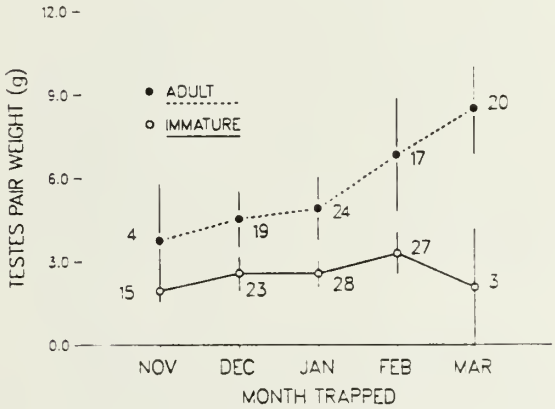

Fig. 4. Mean weights of testes pairs for age classes of wolverine trapped November through March, Yukon 1982–1985. Weights were standardized by soaking testes in water for 24 h. Standard deviations and sample sizes are indicated.

and these age classes are considered as "immature". Age class and month trapped were significant factors in explaining variation in male testes weights (P < 0.01). Testes weights of adults increased in February and March (Fig. 4). Differences existed between age classes in mean length ($F_{2,191}$ = 39.78, P < 0.01) and weight ($F_{2,191}$ = 61.28, P < 0.01) of bacula. However, overlap of these measurements indicate age classifications based on characteristics of bacula are not definitive (Table 2).

Table 2. Bacula measurements for age classes of Yukon wolverine, 1982–1985.

Age class	n	Length (mm)				Weight (g)			
		mean±*SD*	min	max	95% conf. lim.	mean±*SD*	min	max	95% conf. lim.
Young of year	61	73.30±5.07	58.06	84.04	72.04–74.64	1.06±0.31	0.59	2.13	0.98–1.14
Subadult	40	76.19±6.18	62.12	88.40	74.22–78.17	1.28±0.50	0.63	3.13	1.12–1.45
Adult	93	81.05±5.18	56.82	91.72	79.98–82.12	1.96±0.62	0.82	3.35	1.83–2.09

4. Discussion

4.1. Females

Pre-reproductive females were trapped in all months from November through March and the proestrus period could not be determined for wolverine. Induced ovulation is common in mustelids and occurs in mink (*Mustela vison*) and ermine (*Mustela erminea*) (Martinet et al. 1984), polecat (*Mustela putorius*) and skunk (*Mephitis mephitis*) (Mead & Wright 1983), and likely occurs in wolverine. The prolonged estrus characteristic of induced ovulators is usually effected by growth of several follicular waves (Weir & Rowlands 1973). Because many follicles develop but only few actually ovulate (Weir & Rowlands 1973), presence of follicles in ovaries or time of development cannot be construed as evidence that estrus is pre-eminent.

Female wolverine in Yukon did not breed in their first summer and our results are consistent with results of Rausch and Pearson (1972) and Liskop et al. (1981). Of subadults, 7.4% were pregnant, in contrast with the 50.0% (20/40) reported by Rausch & Pearson (1972) and 84.6% (11/13) reported by Liskop et al. (1981). Direct comparison with Rausch & Pearson (1972) is difficult as they classified young of year as "0–15 months" and subadults "16–28 months". Both Rausch & Pearson (1972) and Liskop et al. (1981) used cementum analysis as an aging technique. Wolverine are difficult to age using this method (Banci 1982) and error in reported ages should be considered. However, even assuming that a proportion of subadults were misclassified by age, pregnancy rate for subadult females in our study is the lowest reported for wolverine. Approximately 50% of the 2+ age class were pregnant. Because Rausch & Pearson (1972) and Liskop et al. (1981) lumped 2+ year-old and older females into "adults", age specific comparisons cannot be made. Age of sexual maturity in mustelids varies with nutrition (Mead & Wright 1983). Differences in age of sexual maturity between Yukon (1982–1985) and other areas and periods may reflect differences in nutrition status.

Although methodological differences make some comparisons with other studies difficult, results from mature females imply that differences in reproductive rates exist among wolverine populations. The proportion of adult females pregnant (73.4%) in our sample is less than that found in Alaska and Yukon, 91.8% (90/98) (Rausch & Pearson 1972), and in British Columbia, 88.5% (23/26) (Liskop et al. 1981). Comparison of reproductive rates of wolverine among studies using corpora lutea counts is not possible because the authors did not state whether they included ovaries with no corpora lutea in their calculations. In addition, the utility of this statistic is limited without considering age-specific differences. Rausch & Pearson (1972) found no difference in number of ova shed between first breeders and multiparous females. Our results indicate that reproductive rate increases with age, consistent with age-specific natality described for other mammals (Caughley 1977:83). Because reproduction is age-dependent, differing age compositions of samples between studies could account for some of the differences in estimates of natality.

Unimplanted blastocysts have been found in females killed in October, November and January (Wright & Rausch 1955); in December (Rausch & Pearson 1972); and in February and March (Liskop et al. (1981)). In our sample, pregnant females occurred in all months of the trapping season and indicates that time of implantation occurs at least as early as November. The variation of embryo size emphasizes the variability in timing of implantation and parturition. If a female implants in November, and the active period of pregnancy is 30 to 40 days (Rausch & Pearson 1972), birth would occur in December. This may be an inhospitable time to give birth for many northern mammals but not necessarily for wolverine. Parturition should be timed for maximum survival of

young, likely the time of greatest food availability. Because wolverine are scavengers dependent on ungulate carcasses, food should be more plentiful in winter, and this may be the best season for wolverine reproduction.

Non-pregnant females occurred in sexually mature age classes of wolverine. The proportion of non-pregnant females in age classes 2+ to 5+ years ranged from 7.7 to 46.7%. Pregnancy rate of females 6+ years and older (62.5%) may be less than that of younger adults. This estimate needs to be confirmed with a larger sample size. The relatively high proportion of pregnant adults (73.4%) indicates that most females breed annually, presumably even if they have had a litter the same year. In many mammals, ovulation occurs shortly after parturition (Weir & Rowlands 1973). The presence of follicles in ovaries of post-partum females suggests wolverine females are capable of breeding soon after having young. Reproductive characteristics and success are closely linked to food resources (Robbins 1983:167–206). However, the relationship between habitat productivity and wolverine reproduction is not clear. The oldest female in our study with no evidence of prior breeding was 4+ years. Female wolverine in arctic Alaska that inhabited an area where food was scarce bred but not all produced kits (Magoun 1985). One adult female produced no young in the 3 years she was observed (Magoun 1985). Approximately 50% of monitored females in an area having greater food resources were not pregnant (Hornocker & Hash 1981). Two of 3 radio-collared adult females in Yukon where food was apparently abundant did not reproduce (Banci 1987).

Newborn wolverine kits are altricial (Shilo & Tamarovskaya 1981). By 7 months of age, kits in the wild attain adult weight (Magoun 1985). Rapid growth of young emphasizes the large energy and nutrient contribution made by their mothers. Lactation is energetically very expensive, more so than gestation (Sadleir 1984). Even if a female with kits does breed, such demands may influence her ability to reproduce the following year. Evidence from radio-collared wolverine suggests the proportion of females pregnant determined from reproductive tracts overestimates the proportion of females in the population that will have young. Loss of young may occur before or after birth. Absorbtion of fetuses was observed for 2 of 19 macroscopic *in utero* litters. The proportion of non-detectable losses *in utero* is unknown but likely large, considering the low reproductive success observed in the wild. Loss after parturition (1 kit each from 2 litters of 4) was reported by Pulliainen (1968). The relatively high proportion of adult females pregnant in our study and that found by Rausch & Pearson (1972) and Liskop et al. (1981) suggest reproductive losses occur primarily *in utero* and after implantation. The condition of females before implantation may be the most critical factor determining reproductive success.

Mean litter size from *in utero* fetuses in our study (3.2) exceeds that reported for northern British Columbia (2.6) (Liskop et al. 1981) and is comparable to that reported for Alaska and Yukon (3.5) (Rausch & Pearson 1972). The value for northern British Columbia is based on 5 females and may be inaccurate because of the small sample size. Rausch & Pearson (1972) report a range of 1 to 6 "detectable" fetuses (n = 54 females). Their plot of crown-rump length over time is based on a smaller sample (n = 20 fetuses) and implies "detectable" fetuses includes those that were too small to be easily measured. This range includes fetuses which would be absorbed early and is an overestimate of actual number produced. *In utero* litters in our study ranged from 2 to 4 kits. From 161 dens in Finland, Pulliainen (1968) reported a mean litter size of 2.5, litters of 2 and 4 were rare. In arctic Alaska, from 5 litters a maximum of 2 kits were observed after den abandonment (Magoun 1985).

4.2. Males

Based on evidence of spermatogenesis, Liskop et al. (1981) classified males as mature if testes weighed more than 6.5 g. Using this criterion, in Yukon no subadults were sexually mature, whereas by March all adults were in breeding condition. Rausch & Pearson (1972) noted males were sexually mature at 14–15 months but some did not show evidence of spermatogenesis until 26–27 months. Our results indicate most males, as most females, are not reproductively active until 2+ years of age. Rausch & Pearson (1972) reported a peak in testes weights in June, presumably also indicating the peak in breeding activity. The trend of increase in average weight of testes during early spring is apparent in our data.

Growth of bacula is stimulated by male hormones at the onset of sexual maturity (Wright 1950). Rausch & Pearson (1972) commented on the overlap in bacula weights between age classes and concluded their utility was limited to separating young of year from older animals. Our results using both length and weight of bacula agree with their findings. Extent of

overlap in bacula measurements between young of year and subadults supports an age at sexual maturity of 2+ years for male wolverine. Bacula measurements should not be used as criteria of age without other evidence.

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Home range and habitat use of wolverines Gulo gulo in Yukon, Canada

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Banci, V. and Harestad, A. S. 1990. Home range and habitat use of wolverines *Gulo gulo* in Yukon, Canada. – Holarct. Ecol. 13: 195–200.

Home ranges and habitat use are described for three adult female, one adult male, and one subadult male wolverines in the Kluane Game Sanctuary, Yukon. When long distance excursions are not included, home ranges of wolverines in the Kluane Game Sanctuary were between 76 and 269 km^2 for females and 209 and 269 km^2 for males. Habitat use of females was similar to habitat availability. Males used subalpine coniferous habitats more frequently than other habitat types during winter. Although individual variation in the use of forest cover types, aspects, slopes and elevations was apparent, seasonal use did not differ from availability for each sex. Within the 1590 km^2 study area, three adult males and six adult females were present, corresponding to a density of one resident wolverine 177 km^{-2}.

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Introduction

The wolverine *Gulo gulo* is a carnivore-scavenger of northern ecosystems and is the largest and the least known of mustelids in North America. It occurs at low densities and is a solitary resident of tundra, boreal forest, and mountainous regions. Ungulate carcasses are important food of wolverines in winter, however the wolverine's varied diet attests to its opportunistic nature. In North America, home ranges and movements have been described for wolverines in Montana (Hornocker and Hash 1981), south-central Alaska (Garner 1985, Whitman et al. 1986), and arctic Alaska (Magoun 1985). We report results of the first major field study of wolverines in Canada. Our objectives were to determine size of home range, describe habitat use, and estimate density of wolverines in the Kluane Game Sanctuary of southwest Yukon.

Methods

Study area

The study area (between 139°10′ and 139°45′N, and 61°15′ and 61°30′W, Fig. 1) is in the Ruby Range Ecoregion and partly in the St. Elias Mountains Ecoregion (Oswald and Senyk 1977). The Ruby Range Ecoregion is characterized by rolling hills greater than 900 m in elevation. The St. Elias Mountains Ecoregion is predominately rugged mountains, icefields and glaciers. Within the study area, forests are park-like with canopies that are rarely dense or closed. Elevations range from 762 to 2345 m and treeline is at 1050 m. The climate is typically cold and dry. Mean temperatures recorded at the Burwash Flight Station from January 1983 to March 1986 were −25 to −8°C for January and 11 to 12°C for July. Precipitation ranged from 6 to 14 mm for January and 43 to 121 mm for July.

Vegetation in the Kluane Game Sanctuary was classified by Oswald et al. (1981). The alpine zone contains high elevation terrain and includes areas where the vegetation is low-growing and dominated by willow *Salix* spp., dryas *Dryas* spp., ericaceous shrubs, and lichens. The subalpine zone includes mountainous terrain from below alpine to large valley bottoms. Shrub birch *Betula glandulosa* and willow are prevalent. Sedge and tussock fields occur on wet sites. Below treeline, in the boreal spruce zone, white spruce *Picea glauca* is the climatic climax species but may share dominance with black spruce *Picea mariana*. Balsam poplar *Populus tricho-*

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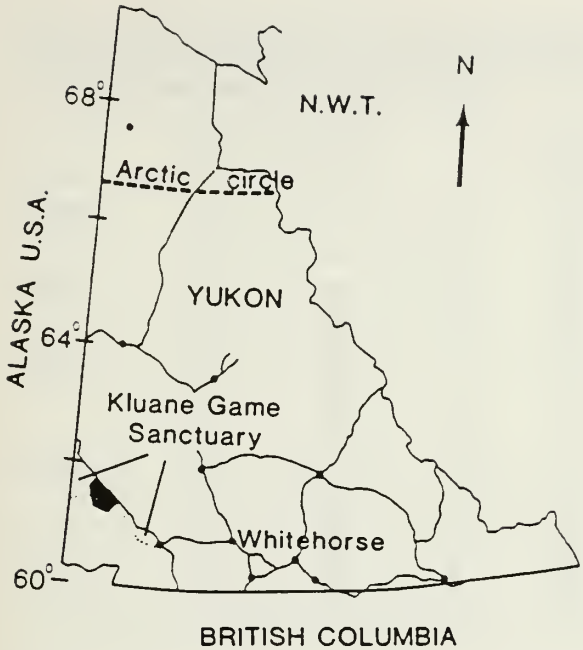

Fig. 1. Location of study area in Kluane Game Sanctuary, Yukon.

carpa occurs sporadically. Understory species are willow, shrub birch, aspen *Populus tremuloides*, soapberry *Shepherdia canadensis*, alder *Alnus incana*, and ericaceous shrubs. Riparian habitat is common in all zones.

The study area supported a diverse prey base, including small herbivores (Sciuridae, Lagomorpha, and Microtinae) and ungulates (moose *Alces alces*, woodland caribou *Rangifer tarandus*, Dall's sheep *Ovis dalli*, and mountain goat *Oreamnos americanus*). Lynx *Lynx canadensis*, red fox *Vulpes fulva*, coyote *Canis latrans*, wolf *Canis lupus*, and grizzly bear *Ursus arctos* were common. Black bear *Ursus americanus* were rare. Other mustelids present in the area were ermine *Mustela erminea* and pine marten *Martes americana*. Because the Kluane Game Sanctuary has been closed to hunting and trapping since its establishment in 1943, the wolverine population we studied was unharvested.

Field studies

We live-trapped wolverines during winters 1983–84 and 1984–85 in an 1800 km^2 area using steel box and padded leg-hold traps. Wolverines were immobilized with ketamine hydrochloride (Rogar/STB Ltd.) and xylazine hydrochloride (Haver-Lockhart). An upper premolar was aged by cementum analysis. Based on the timing of sexual maturity, wolverines 0–1 years old were classed as "young of year", 1–2 years as "subadult", and 2 years and older as "adult". Radio transmitter collars (Telonics Inc.: 148–150 mhz) and ear tags (Nasco Inc.) were attached before wolverines were released. A Piper Super Cub or Cessna 180 aircraft with a null antenna (Telonics Inc.) mounted on each wing strut was used to locate wolverines on average once every 10 d, from January 1984 through March 1986.

Locations were plotted onto 1:50,000 topographic maps during tracking flights and accompanied by a description of habitat type and percent forest cover. Tracks and sightings of wolverines were recorded during flights and in areas accessed by snowmachine. Incidental observations were collected from local residents, Kluane National Park personnel, pilots, and other biologists. Unmarked wolverines were classified as residents if they were present in an area over the duration of the study.

Analyses

Home range size was calculated using the minimum home range method as modified by Harestad (1981). Winter included November through April, and summer May through October, coinciding with snow-present and snow-free periods, respectively. Classification of habitat included three zones: alpine, subalpine, and boreal forest. Within each zone, there was a maximum of five possible habitat types: coniferous, mixed, shrub, grass-sedge and talus-rock. For each location, slope and aspect in degrees were calculated and the elevation recorded from maps. Aspect was categorized as "N" (316–45°), "E" (46–135°), "S" (136–225°), "W" (226–315°), and "flat". Classification of forest cover was: < 20%, sparse; 20–50%, scattered; 50–80%, open; and > 80%, closed (Oswald et al. 1981). Riparian habitat was defined as the area 0.05 km on either side of water bodies and included all streams, rivers, sand bars, deltas, and permanent glacial ponds.

To determine habitat availability, computer generated random locations were overlayed on each home range (Marcum and Loftsgaarden 1980) and for each point, zone and habitat type were recorded. The occurrence of riparian habitat was recorded independently of zone and habitat type. To obtain adequate sample sizes, this process was repeated within each home range until estimates of the relative frequencies of available habitat types remained constant. Use of habitats was compared to availability using a χ^2 goodness of fit test (Neu et al. 1974). Bonferroni simultaneous confidence intervals for the proportions of habitat types used (p) were constructed ($p \leq 0.05$, Byers and Steinhorst 1984). For riparian habitat, use was compared to availability using standard Z-tests. The use of elevations, slopes, aspects and percent forest cover was compared between sexes and seasons using Mann-Whitney U-tests.

Results

Ten wolverines, five males (three adults, one subadult, one young of year) and five females (three adults, two young of year), were captured over the two winters. One adult male was lost immediately after release and

Tab. 1. Home ranges of wolverines enclosing between 90–100% of closest locations for three adult females (F384, F484, F584), one subadult male (M285), and one adult male (M385) in Kluane Game Sanctuary, Yukon 1983–1986.

	% Home range	Size (km^2)	n	% of total area
F384	100	139	39	100
	97	76	38	55
	90	47	35	34
F484	100	202	30	100
	97	157	29	78
	90	134	27	67
F584	100	343	33	100
	97	269	32	78
	94	153	31	45
	90	128	29	37
M285	100	526	21	100
	92	412	20	78
	90	283	18	54
M385	100	238	29	100
	97	209	28	88
	90	188	26	79

one adult female was lost after 10 months of tracking because of collar malfunctions. Two wolverines moved outside the Kluane Game Sanctuary and were killed by trappers, four died of apparent natural causes, and two survived to the end of the study. One of the adult females, F384, had kits during the study. Nine wolverines were tracked from 21 to 494 d. Home range and habitat use are described for five individuals having a minimum of 295 d of air time: three adult females, one adult male, and one subadult male.

Home range use

The 100% home ranges of the five wolverine were between 139 and 526 km^2. Home ranges which contained 90% of closest locations represented 21–66% reductions in size from the 100% home range (Tab. 1) and enclosed areas of intensive use. Females made one to two long distance movements, all of which occurred during summer. We considered these excursions temporary movements out of the usual area of use. When excursions were not included, the yearly home ranges for females without kits, F484 and F584, were similar, 157 km^2 and 153 km^2, respectively. The yearly home range for F384, without her one excursion, was 76 km^2. The home range size for the subadult male, M285, was underestimated because he had left the study area and could not be relocated from November to December of 1985. No excursions were apparent for M385, the adult male.

Because we could not assume that yearly home ranges were constant, seasonal home ranges were not estimated unless months of contact were consecutive.

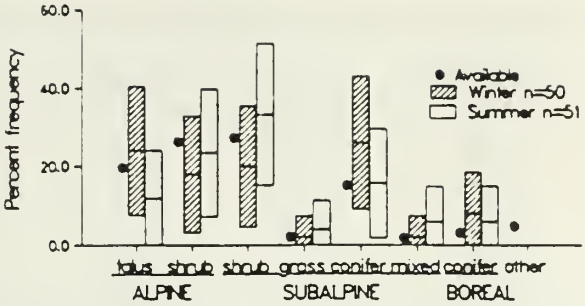

Fig. 2. Use of habitat types by 3 adult female wolverines in Kluane Game Sanctuary, Yukon 1984–1986. Use did not differ from availability during winter (χ^2 = 12.98, 7 df, $p > 0.05$) nor summer (χ^2 = 11.74, 7 df, $p > 0.05$). Horizontal lines represent the mean proportion used and bars are 95% Bonferroni confidence intervals ($p \leq 0.05$). 'Other' is minor habitat types.

Winter estimates were not available for F384, F484 and M285. F384's summer home range was reduced from 118 km^2 to 62 km^2 (n = 22) when excursions were not included. F484's summer home range, not including her one excursion, was 110 km^2 (n = 17), reduced from 141 km^2. A summer home range size of 210 km^2 (n = 11) for F584 was attributable to excursions made in July and August of 1985. After discounting these movements, her summer home range, 82 km^2 (n = 9), was smaller than her winter home range, 119 km^2 (n = 11). The subadult male, M285, had the largest summer range, 437 km^2 (n = 10). M385, an adult, had the smallest summer home range, 46 km^2 (n = 12). The following winter, he used a home range of 146 km^2 (n = 13). Overlap of the home ranges of M285 and M385 was extensive.

The denning behaviour of F384 was evident from a reduction in movements and a concentration of locations between April and June of 1984. From November 1984 through early January 1985, this female again re-

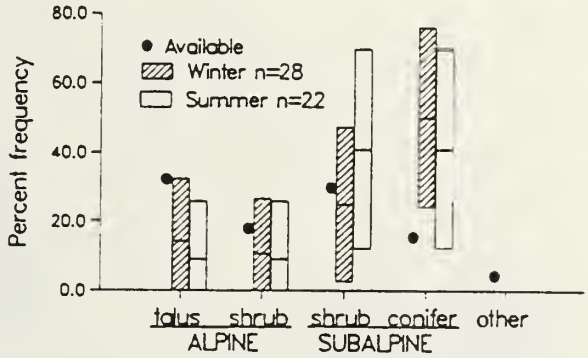

Fig. 3. Use of habitat types by 2 male wolverines in Kluane Game Sanctuary, Yukon 1985–1986. Use differed from availability during winter (χ^2 = 11.61, 4 df, $p \leq 0.05$) and summer (χ^2 = 15.72, 4 df, $p \leq 0.05$). Horizontal lines represent the mean proportion used and bars are 95% Bonferroni confidence intervals ($p \leq 0.05$). 'Other' is minor habitat types.

Tab. 2. Comparisons of seasonal use of forest cover types, aspects, slopes, and elevations for wolverines in Kluane Game Sanctuary, Yukon 1984–1986[a].

	n(Winter)[b]	n(Summer)[c]	% Cover	Aspect	Slope	Elevation
F384	16	23	0.20	0.29	2.68**	1.87*
F484	12	17	0.87	0.50	0.27	0.00
F584	21	11	1.66*	0.52	0.60	1.39
M285	10	10	1.37	1.32	0.83	1.20
M385	17	11	0.47	0.07	1.06	1.88*
Females[d]	49	51	1.61	0.90	2.36*	0.27
Males[e]	27	21	1.44	0.94	0.23	0.62

* $p \leq 0.10$, * $p < 0.05$, ** $p < 0.01$, (else $p > 0.10$).
[a]Results are z-values for Mann-Whitney U-tests, [b]November–April, [c]May–October, [d]F384, F484, F585, [e]M285, M385.

stricted her activity to a 14 km² area. At this time, however, she relied on baited traps. She died after the fourth recapture. She had external lacerations and an autopsy indicated parasitic infestations in all major organs. At first capture in February 1984, and before having kits, she weighed 11.0 kg, compared to 8.2 kg at recapture in December 1984.

Habitat use

Among females, the yearly use of alpine shrub habitat by F484 was less than that available (available $p = 0.18$, used $0.00 \leq p \leq 0.12$). Yearly use of other habitats by females was not different from availability. Seasonal use of habitat types by females did not differ from availability (Fig. 2). Males used less alpine talus habitat in summer and more subalpine coniferous habitat in winter than expected if use was proportional to availability (Fig. 3). Use of riparian habitat did not differ from availability for all males and females (Z-test, $p > 0.20$). Although individual differences were apparent, the seasonal use of forest cover types, aspects and elevations did not differ from availability for each sex (Tab. 2). Females used steeper slopes (> 61°) to a greater extent in summer but this was attributable to F384 (Tab. 2). Elevations used by wolverines comprised the range of elevations that occurred in the study area.

Wolverine density

During 1983 and 1984, 88 observations of unmarked wolverines were obtained. Three unmarked female wolverines (number of trails and sightings), F1 (5), F2 (12), F3 (9), and 2 unmarked males, M1 (10) and M2 (9), were classed as residents. M1, F1 and F2 were captured in padded foothold traps but escaped. Only F3 was not sighted. The large size of both unmarked males and their residency suggested they were adults. The age classes of the females were unknown but because all three were present in the area for a minimum of two yr, they would have been adults by the end of the study. Home ranges of unmarked adult wolverines were esti-

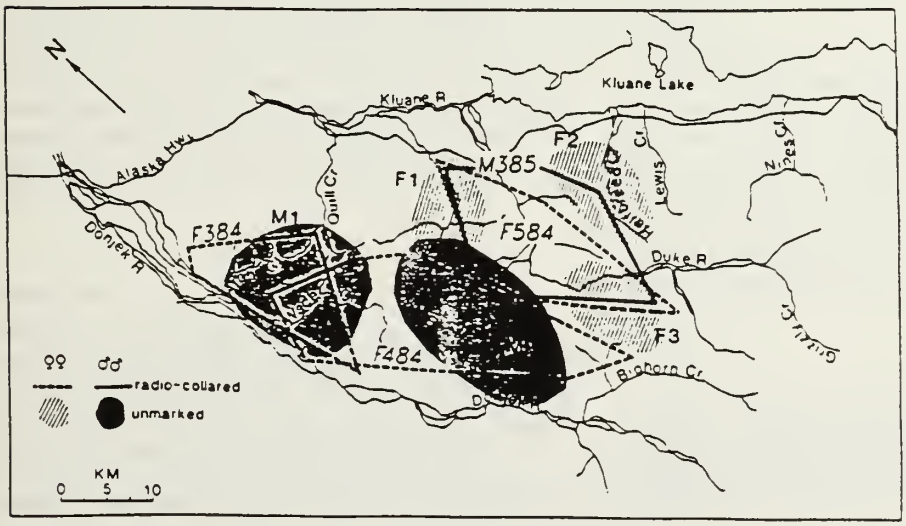

Fig. 4. Yearly home ranges of adult wolverines resident in Kluane Game Sanctuary, Yukon 1983–1986 based on 100% home ranges of radio-collared wolverines and home ranges of unmarked wolverines estimated from tracks and sightings.

mated using observed locations (Fig. 4). Including collared wolverines, three adult males and six adult females were present within the 1590 km^2 that was monitored during the three yr of the study. This corresponds to a density of 1 female 265 km^{-2} and 1 male 530 km^{-2}, or 1 resident wolverine 177 km^{-2}. We also calculated wolverine density by assuming home ranges were exclusive within adult sexes. Using a mean home range of 157 km^2 for females and 238 km^2 for males allows 10 female and seven male residents in the study area, corresponding to a density of 1 resident wolverine 93 km^{-2}.

Discussion

Home ranges

Yearly home ranges of the adult females without kits (153 and 157 km^2) in Yukon were smaller than those of adult females in Montana, a mean of 388 km^2 (Hornocker and Hash 1981), but within the range of females in arctic Alaska, a mean of 103 km^2, and a range of 53–232 km^2 (Magoun 1985). The yearly home range size of the female with kits (76 km^2) was similar to home ranges reported from other areas. Lactating females and those with kits had yearly home ranges of 100 km^2 in Montana (Hornocker and Hash 1981), a mean of 105 km^2 in south-central Alaska (Whitman et al. 1986), and a mean of 70 km^2 in arctic Alaska (Magoun 1985).

The yearly home range of M385 (238 km^2), the adult male, was smaller than the home ranges of adult males in Montana (mean of 422 km^2, Hornocker and Hash 1981), arctic Alaska (mean of 666 km^2, range 488–917 km^2, Magoun 1985), and 637 km^2 for a male in south-central Alaska (Gardner 1985). Home ranges of adult male wolverines typically overlap those of several females (Gardner 1985, Magoun 1985). During spring and summer, males increase their home range size and movements, apparently because of breeding activity (Hornocker and Hash 1981, Magoun 1985). M385's summer home range (46 km^2) was one third of the size of area used in winter, and smaller than the summer home ranges of the three radio-collared females. Because abundant prey provided high quality habitat, we believe his requirements were satisfied by a smaller home range.

Habitat use

Habitat use by female wolverines was not significantly different from habitat availability. Habitat use by the adult and the subadult male were similar, partly because of the extensive overlap of their home ranges. We attribute their greater use of subalpine coniferous habitats in winter to the presence of ungulate carcasses in these habitats. Individual variation in the use of forest cover types, aspects, slopes, and elevations by wolverines was apparent. The use of higher elevations in summer and lower elevations in winter was observed for only the denning female and the adult male. Gardner (1985) hypothesized that the use of higher elevations during summer by wolverines in Alaska was due to concentrations of ground squirrels in alpine areas. Hornocker and Hash (1981) reported that wolverines in Montana moved to higher elevations in summer because of high temperatures. In the Kluane Game Sanctuary, non-ungulate prey in alpine habitats during summer consisted of little besides pika and microtines. Summers in Kluane are generally cool and temperatures are lower than those reported for Montana. The seasonal shifts in elevation by wolverines in Montana and Alaska appear to be responses to local environmental conditions and did not occur for most wolverines in the Kluane Game Sanctuary during our study.

Wolverine density

Methods used by various authors for calculating wolverine densities are not consistent. By using tracks and sightings, Quick (1953) estimated a density of 1 resident wolverine 207 km^{-2} for a trapline in northern British Columbia. Hornocker and Hash (1981) estimated a density of 1 wolverine 65 km^{-2} in their 1300 km^2 study area in Montana. This density was based on all wolverines they believed were present and may have included juveniles. Whitman and Ballard (1983) reported a density of 1 wolverine 209 km^{-2}, including kits but not juveniles, for the Susitna River Basin in southcentral Alaska. They assumed the home range observed for 1 adult male (627 km^2) in their study area was characteristic of all adult males. Using mean home range sizes and estimates of productivity, Magoun (1985) reported densities of 1 wolverine 48 km^{-2} to 1 wolverine 139 km^{-2} for a resident fall population in arctic Alaska, including adults, daughters which settled next to the natal area, and kits.

Our estimate of 1 resident wolverine 93 km^{-2}, calculated from mean home range size, includes areas where wolverines were not present. Because the entire study area was not equal in habitat quality, and habitat saturation by wolverines was unlikely, this density is likely an over-estimate. By considering wolverines known to reside in the 1590 km^2 study area, we estimated a density of 1 resident wolverine 177 km^{-2}. Densities of wolverines in the southern Yukon are similar to densities of wolverines in south-central Alaska and northern British Columbia.

Acknowledgements – Support was provided by Yukon Department of Renewable Resources, World Wildlife Fund (Canada), Department of Indian and Northern Affairs, Canadian Wildlife Service, and the Natural Sciences and Engineering Research Council of Canada. We thank B. Slough, H. Jessup and P. Merchant for their assistance.

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Deems and Pursely 1983

WOLVERINE
(*Gulo gulo*)

DESCRIPTION: The wolverine resembles a small bear. It is distinguished by an arched back, short bushy tail, relatively long legs, and large feet. The pelage is long, usually dark brown (lighter on the head) with light-colored stripes extending from the shoulders, along the sides, joining on the rump and base of the tail. The head is broad, tapering to a prominent black muzzle. The ears are wide-set, relatively small and rounded. Each foot has 5 toes with relatively long, non-retractable claws. Sexes are similar in appearance except males are larger than females. Adults attain total lengths of 36 to 41 inches (91 - 104 cm) including the 7 to 9 inch (18 - 23 cm) tail and weigh 35 to 60 pounds (16 - 27 kg). The skull has 38 teeth. There are 4 mammae.

HABITAT: Historically, wolverines inhabited most of the boreal forests in North America. In recent times the wolverine range's southern boundaries have moved northward and today it is most common in Alaska and Canada in areas between the timberline and the arctic coast. In the conterminious U.S. wolverines inhabit the higher ranges of the Rocky Mountains in Idaho. Montana, Wyoming, Colorado and possibly Utah. They also occur in the higher elevations of the Cascade Mountains in Washington and Oregon, in the Sierra Mountains and upper Coast Range in California.

FEEDING HABITS: Wolverines are omnivores. Their diet includes a wide variety of plant material, including fruits, berries, nuts and roots, as well as animals, including small mammals, birds, fish and carrion. Wolverines are known to attack larger ungulates such as deer, goats, sheep and caribou.

BEHAVIOR: Wolverines primarily are solitary and may be active at any hour of the day or night. They are extremely powerful and aggressive animals for their size. Their feats of strength are legendary among trappers who view the wolverine as a furbearer, trap robber, and cabin plunderer. Wolverines are extremely territorial and therefore do not occur in high densities in any habitat type or area.

REPRODUCTION: The breeding season is late April to September. Implantation is delayed and gestation is extremely variable. Implantation usually occurs in January or February and parturition occurs about 60 days later. Litter sizes range from 1 to 5 (average is 2 or 3) and the altricial newborn have fuzzy, creamy-white coats. Dens are located in sheltered areas in rocky out-crops, under logs or tree roots. The young are weaned at about 8 or 9 weeks of age and remain with the mother through their first winter but disperse the following spring. Females are sexually mature and capable of breeding in their second year. Males may not breed until later.

POPULATION STATUS: North America's wolverine population is generally stable with the exception of eastern Canada where habitat loss is a significant factor. Even though pelt prices have increased progressively and substantially during the last decade, the harvest has remained relatively constant.

UTILIZATION: Wolverine pelts are prized as parka trim and sub-zero clothing because of their warmth and ability to remain frost free. Wolverines are taken primarily by trappers, but in some northern areas they are hunted as trophy game animals. In recent years, the annual North American (Alaska and Canada) harvest of wolverines has

remained relatively stable at about 2,000 pelts, and the total annual harvest values range between $250,000 and $300,000.

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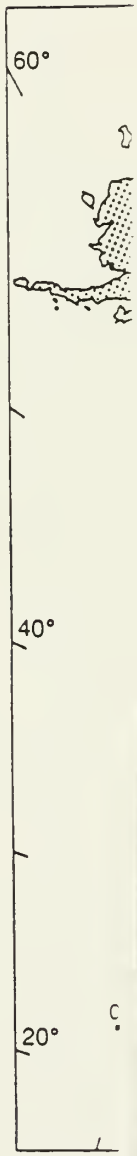
Map 20.



Map 20. The Range of the Wolverine in the United States and Canada.

Fig. 20 The Management Status of the Wolverine in the United States and Canada

STATES, PROVINCES AND TERRITORIES	Present	Total Protection	Hunting Season	Trapping Season	Year-Round Harvesting	Limited Harvesting	Food Resource	Habitat Management	Population Inventories	Special Regulations	Private Lands Leased
United States											
Alabama											
Alaska	●		●	●		●			●		
Arizona											
Arkansas											
California	●	●									
Colorado	●	●									
Connecticut											
Delaware											
Florida											
Georgia											
Idaho	●	●									
Illinois											
Indiana											
Iowa											
Kansas											
Kentucky											
Louisiana											
Maine											
Maryland											
Massachusetts											
Michigan											
Minnesota		●									
Mississippi											
Missouri											
Montana	●			●		●			●	●	
Nebraska											
Nevada											
New Hampshire											
New Jersey											
New Mexico											
New York											
North Carolina											

STATES, PROVINCES AND TERRITORIES	Present	Total Protection	Hunting Season	Trapping Season	Year-Round Harvesting	Limited Harvesting	Food Resource	Habitat Management	Population Inventories	Special Regulations	Private Lands Leased
United States (Cont'd)											
North Dakota											
Ohio											
Oklahoma											
Oregon	●	●									
Pennsylvania											
Rhode Island											
South Carolina											
South Dakota											
Tennessee											
Texas											
Utah		●									
Vermont											
Virginia											
Washington	●	●									
West Virginia											
Wisconsin											
Wyoming	●	●									
Total (United States)	8	8	1	2	0	2	0	0	2	1	0
Canada											
Alberta	●		●	●						●	
British Columbia	●		●	●		●					●
Manitoba	●			●		●				●	
New Brunswick											
Newfoundland	●	●									
Northwest Territories	●			●		●					
Nova Scotia											
Ontario	●			●		●			●		
Prince Edward Island											
Quebec	●			●		●					
Saskatchewan	●			●	●						
Yukon Territory	●		●	●		●				●	
Total (Canada)	9	1	3	8	1	6	0	0	1	3	1

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LONG DISTANCE MOVEMENT BY AN ADULT WOLVERINE

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Timing and extent of dispersal by juvenile (<15 months) wolverines (*Gulo gulo*) (Gardner, 1985; Magoun, 1985) and movement patterns by resident adult wolverines (Gardner, 1985; Hornocker and Hash, 1981; Magoun, 1985) have been described. However, there are few data concerning movement patterns of wolverines that are sexually mature but not residents of an area. This note describes a record 378-km movement by an adult male wolverine from southcentral Alaska to the Yukon Territory, Canada.

On 6 March 1981, an 18-kg, 2-year-old male wolverine (M5) was captured and radio-collared along the Susitna River (62°45'N, 147°45'W) in southcental Alaska. Between 6 and 25 March, M5 used an area within the annual home range of resident M1, a 7-year-old male which we had been monitoring since May 1980. In March, the home ranges (Mohr, 1947) of both M1 and M5, based on six locations for each, were within M1's annual home range and were contiguous and comparable in size: 80 and 89 km^2 for M1 and M5, respectively.

Between 25 March and 15 April 1981, M5 left the area and radio contact was lost. M5 was trapped on 29 November 1982, along the White River in Yukon Territory, Canada (62°15'N, 140°30'W), a straight-line distance of 378 km east from its collaring location. The largest previously recorded movement was approximately 300 km during a 5-month period, by a yearling female of unknown resident status (Magoun, 1985). Juvenile wolverines disperse 30 to 100 km from their natal range (Gardner, 1985; Magoun, 1985).

In southcentral Alaska, resident adult males appear to have mutually exclusive home ranges (Gardner, 1985). Since M5 was located within resident M1's annual home range, there may have been social pressure from M1 causing M5 to leave the area. We did not know the length of time M5 resided within M1's annual home range prior to capture. However, during the period of coresidence, which lasted at least 19 days, M1 may have been tolerating M5's presence or may not have encountered him.

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Distribution of the Wolverine in Idaho as Determined by Mail Questionnaire

Abstract

The wolverine was once thought to be extinct in Idaho, but reports of its occurrence persist. In order to better determine the status and distribution of this rare species, questionnaires were sent to biologists and trappers statewide in 1985. Responses to the questionnaires resulted in 10 confirmed and 89 probable reports of wolverines in Idaho between 1960 and 1987. At least three areas in the state (Selkirk Mountains, Lochsa and Kelly Creek drainages, Sawtooth and Smoky Mountains) appear to contain wolverine populations. These areas can be characterized as remote, mountainous habitat with little human disturbance. The present-day distribution of the wolverine in Idaho is probably in the mountainous portions of the state from the South Fork of the Boise River north to the Canadian border. Although this survey has provided insights into the current distribution of the wolverine in Idaho, detailed analysis on population status and ecology are needed.

Introduction

Wolverine (*Gulo gulo*) numbers declined steadily in the contiguous United States (Wilson 1982) after the late 1800s. Today, they are uncommon in the lower 48 states and likely only occur in Oregon, Washington, California, Idaho, Montana, and Wyoming. Davis (1939) believed the wolverine to be extinct in Idaho by the 1930s. Pengelly (1951) summarized seven records of wolverine in Idaho from 1930 to 1949. These records were primarily from the northern Idaho counties of Bonner, Boundary, Kootenai, and Shoshone. The next verified records of wolverines in the state were two kills, one in northern Idaho in 1953 and one in southern Idaho in 1954.

Larrison and Johnson (1981) considered the wolverine to be rare and restricted in distribution to areas north of the Salmon River Mountains and to the mountains of southeastern Idaho. Because of its restricted distribution and apparent rarity in Idaho, the Idaho Department of Fish and Game has classified the wolverine as a protected species since 1965. In addition, Region 1 of the U.S. Forest Service, which includes northern Idaho, and the U.S. Bureau of Land Management in Idaho have designated the wolverine as a Sensitive Species. The U.S. Fish and Wildlife Service, under the authority of the Endangered Species Act, has listed the wolverine as a candidate for federal listing as a threatened or endangered species (U.S. Fish and Wildlife Service 1985). To better determine the status and distribution of the wolverine in Idaho, I mailed questionnaires to wildlife biologists and registered trappers throughout Idaho in 1985. The purpose of this paper is to report the results of the 1985 survey.

Methods

During May 1985, questionnaires on wolverine sightings were mailed to all Idaho Department of Fish and Game biologists, conservation officers, and land managers; wildlife biologists in Idaho employed by the U.S. Forest Service, U.S. Bureau of Land Management, U.S. Bureau of Reclamation, and the U.S. Fish and Wildlife Service; academicians and graduate students in biology, zoology, and wildlife departments at Idaho universities and colleges; Nongame Citizens Advisory Committees; the National Audubon Society chapters in Idaho; and state park managers. Concurrently, similar questionnaires were mailed to trappers licensed by the Idaho Department of Fish and Game.

The questionnaire sent to biologists asked respondents to provide information on the date, location (place name, county, latitude/longitude or township-range-section), habitat type, and type of observation (animal, tracks, scat) they had made, if any, during the last 25 years. Biologists were also asked to provide the name, address, and phone number of other people they knew who had information on wolverine sightings in the state.

Each licensed trapper was sent a cover letter explaining the purpose of the wolverine survey along with an addressed and postage-paid postcard for them to return with information on wolverine sightings. The postcard provided them with space to list their name, address, and telephone number; their general trapping area; a "yes" or "no" on whether they had trapped or seen wolverines or wolverine sign during the last 25 years; and the date and area where wolverines or sign had been observed.

Follow-up telephone calls were made to all individuals (biologists and trappers) that responded positively to the wolverine survey. Confirmed wolverine reports consisted of either a photograph or a carcass. For those reports that were not confirmed (i.e., sightings of wolverines or tracks), respondents were asked for a description of the animal, their level of confidence that they had seen a wolverine or tracks of a wolverine, whether they had previously seen a wolverine, the distance and amount of time of their observation, and their amount of experience as a biologist or trapper. If the observer lacked confidence in his/her observation, poorly described the animal, or saw it for a short time span and/or at a great distance, I did not include the wolverine observation in this report. Sightings of wolverines or wolverine tracks included in this paper are referred to as probable reports.

Results and Discussion

One hundred eighty-five of the 296 biologists who were mailed the questionnaire responded to the survey for a return rate of 62.5 percent (Table 1). Thirty-seven of these 185 reponses reported observations of wolverines or wolverine sign. Thirty-five of 427 responding trappers reported observations of wolverines or wolverine sign. Some positive responses from biologists and trappers included information on more than one wolverine report. Thirty-five positive reports returned by biologists or trappers were not included in this report due to insufficient information or lack of credibility in the report.

The survey resulted in only 10 confirmed reports of wolverine in Idaho between 1960 and 1986 (Table 1, Figure 1).[1] Eight of these 10 reports came from northern Idaho north of the Lochsa River, and all but two reports were from national forest lands. Five of the reports occurred between 1960 and 1975 while the other half occurred between 1976 and 1986.

I documented 89 probable reports of wolverines or wolverine tracks between 1960 and February 1987 (Table 1, Figure 1). Nine of these reports (10%) occurred from 1960-1969, 28 (32%) from 1970-1979, and 52 (58%) from 1980-1987. Twenty-one percent of the probable reports were from Bonner and Boundary counties in extreme northern Idaho. Eighteen percent of the reports occurred in the north-central counties of Clearwater and Idaho, and another 22 percent came from a cluster of south-central counties (Custer, Elmore, Blaine, Camas, and Boise).

At least three areas in Idaho, from which confirmed and probable reports were received, appear to contain wolverines. These areas are the Selkirk Mountains adjacent to and north of Priest Lake, the Lochsa and Kelly Creek drainages, and the headwaters of the South Fork and Middle Forks of the Boise River (i.e., Sawtooth-Smoky Mountains) (Figure 1). Several confirmed reports also occurred in the Purcell Mountains north of the Kootenai River, but all of these reports were prior to 1965. Because the longevity of wolverines in the wild is 8-10 years (Wilson 1982), these reports were not indicative of present-day occupancy by wolverines.

Concentrations of probable reports indicated that wolverines also likely occur in Fremont County adjacent to Yellowstone National Park and in the upper St. Joe and Coeur d'Alene River drainages. The Selway and Salmon River drainages in central Idaho were conspicuously absent of any confirmed reports and contained only a few probable reports. The lack of wolverine reports in these areas may reflect their roadless nature and low density of people, particularly biologists and trappers. If we assume that wolverines do occur in these areas, then the present-day distribution of wolverines in Idaho is in the mountainous portions of the state from the South Fork of the Boise River north to the Canadian border.

In a study of wolverines in western Montana, Hornocker and Hash (1981) concluded that wilderness or remote country where human activity was minimal appeared essential to maintaining

[1]Information on the observer's name, affiliation, date of observation, and exact location of observation for confirmed and probable reports is available from the author on request.

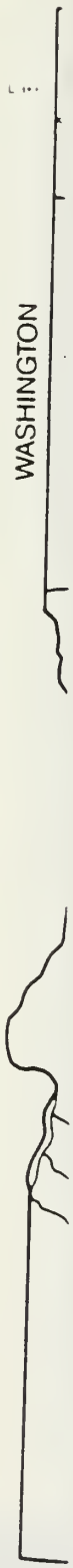

Figure 1. 1

Figure 1. Distribution of wolverine reports in Idaho, 1960-1987. See text for definition of confirmed and probable reports.

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WOLVERINE

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The wolverine (*Gulo gulo*) is the largest terrestrial member of the Mustelidae. The scientific name originated from the Latin word *gulosus* (gluttonous) from *gula* (throat). Taxonomists historically recognized differences between animals from North America and Eurasia, but authorities now acknowledge only one species (Walker 1975, Honacki et al. 1982). Various common names include devil bear, carcajou, skunk bear, and devil beast.

DESCRIPTION

The wolverine resembles a small bear in general appearance except for the bushy tail. It is compact and strongly built, with short thick skeletal structures and heavy musculature, and has a broad head, a short stout neck, and relatively short legs. Adult head-body length ranges from 65 to 105 cm (25.6-41 inches) and tail length ranges from 17 to 26 cm (6.7-10 inches) (Stroganov 1969). The feet are proportionately large and well adapted for deep snow travel, digging, and climbing. Each foot has five toes with strong semiretractile claws that are sharply curved and about 23 cm (0.8-1.2 inches) long. Dense, stiff, bristlelike hair occurs between the toes and around the pads during winter but is quite diminished during summer. Adult forefeet leave circular tracks (Fig. 1) that may be 7-8 cm (2.8-3.2 inches) × 8-9 cm (3.2-3.5 inches) long. The hindfeet are slightly smaller and lack the characteristic division of the primary sole pads of the forefeet (Jackson 1961). The third digit is longest on the hindfeet and the fourth is longest on the forefeet (Wilson 1982).

The pelage is composed of dense, woolly, kinky underfur about 2-3 cm long and coarse, stiff guard hairs about 6-10 cm (2.4-4 inches) long. The fur is short, thick, and uniform on the head and becomes progressively longer posteriorly. The ears are fully furred with extremely short underfur and somewhat longer guard hairs. Wolverine fur has long been valued and widely used in the Arctic and Subarctic as ruffs or trim on parkas and other garments. Hardy (1948) compared the icing characteristics of wolverine, coyote (*Canis latrans*), and gray wolf (*Canis lupus*) fur, and showed that ice crystals formed in the underfur of wolverine fur but that guard hairs remained free from ice. In contrast, wolf fur and coyote fur became matted and covered with chunks of ice. Quick (1952) reported that rime ice or frost from a person's breath forms on wolverine fur parka trim but may be easily brushed away; frost on other furs cannot be brushed or shaken off. Its relative rareness, beauty, and frosting characteristics combine to make wolverine pelts unique and quite valuable.

The background color of wolverine fur varies considerably among individuals, from a medium brown to almost black. Body markings are less variable. A lighter contrasting facial mask sometimes appears with a lighter upper body stripe that extends from the head or shoulders to the rump area and may merge into the tail. Color of the lateral stripe is generally blondish, but the degree of contrast varies among the body color, facial mask, and body stripe. Most specimens display white or light tan patch markings on the throat and chest; these range from one or more small spots to larger, irregularly shaped areas. Occasionally, one or both forepaws and legs may be marked with white or blond areas. Wolverines with one or more white toes are relatively common in the Northwest Territories, and white wolverine pelts are sometimes taken (A. Gunn, pers. commun.). Such pelts are cream-yellow with brownish feet.

Wolverines have anal musk glands characteristic of the mustelids which emit a tannish yellow, highly odoriferous secretion through small lateral openings located just inside the anal orifice. Coues (1877) commented that the glands are about the size of a walnut and that the scent is highly fetid.

Sexual dimorphism in body size exists, with females averaging 10% less in linear measurements and about 30% less in weight (Hall 1981). Adult weights range from 14 to 27.5 kg (31-61 pounds) for males and from 7 to 14 kg (15-31 pounds) for females (Walker 1975). The average weight for a Montana sample of 24 livetrapped research animals was 12.7 kg (28 pounds) for males and 8.3 kg (18 pounds) for females; the largest male was 15.9 kg (35 pounds) (Hornocker and Hash 1981). Twenty-six wolverines captured in northwestern Alaska weighed an average of 14.1 kg (31 pounds) and 9.9 kg (22 pounds) for males and females respectively; the largest male weighed 15.9 kg (Magoun 1985).

Wolverines have small eyes and their sight is relatively poor (Jackson 1961). An acute sense of smell enables the detection of humans or food over long distances with favorable air currents. Wolverines can locate carrion beneath 1-2 m (40-80 inches) of snow (Hornocker and Hash 1981).

The wolverine's skull is massive compared with that of other mustelids, canids, or felids of similar size. Its dental and mandibular structure is extremely strong and capable of crushing all but the larger bones of mammals up to the size of an adult moose (*Alces alces*). The teeth are generally thicker and stronger than those of similar-size predators. The upper/lower dental formula is: incisors, 3/3; canines, 1/1; premolars, 4/4; molars, 1/2; a total of 38 teeth, the same as the marten (*Martes americana*) and fisher (*M. pennanti*). Broken incisors and canines are commonly seen in older animals, apparently the result of chewing on bones or traps. General tooth wear is apparent in adults more than 5-6 years old.

Fig. 1. Impression of a wolverine's forefoot in snow. (Photo: H. Hash.)

Fig. 2. Distribution and harvest density of the wolverine (*Gulo gulo*) in Canada and the United States for the 1983–84 trapping and hunting seasons (based on a survey by M. Novak and A. J. Satterthwaite, Ontario Minist. Nat. Resour.). *Legend:* (A) ≤ 2,500 km²/animal harvested (area = 1,933,000 km²); (B) 2,501–10,000 km²/animal (1,669,000 km²); (C) ≥ 10,001 km²/animal (3,621,000 km²); (D) no harvest (1,203,000 km²). Total current North American range is 8,426,000 km². Historical (c. 1700) distribution, shown by dashed line, occupied 12,600,000 km². (Sources: Jackson 1954, Peterson 1966, Schorger 1968, Nowak 1973, Van Zyll de Jong 1975, Johnson 1977, Kelsall 1981, Wilson 1982). Inset shows Eurasian distribution (Source: Banfield 1974). (2.59 km² = 1 mile²)

DISTRIBUTION

The wolverine has a vast circumboreal distribution (Fig. 2). Wolverines occur from Scandinavia across the taiga and forest–tundra zones of Eurasia (Wilson 1982). Ognev (1935) and Stroganov (1969) presented extensive distribution records for the Soviet Union. Kvam et al. (1984) reported on the status and distribution of wolverine populations in Norway, with reference to connections with neighboring Swedish populations.

The wolverine is believed to have evolved in Eurasia and migrated from Asia to North America across the Bering Strait during the mid-Pleistocene era (Kurtén 1968, Irving 1972). The historical North American distribution included much of the northern part of the continent southward to the northernmost tier of the United States from Maine to Washington state (i.e., the southern boundary of the range was roughly the 38th parallel) (Fig. 2). The historical range apparently extended southward in conjunction with the prairie–forest ecotones down the Rocky Mountains to Arizona and New Mexico at the higher elevations. Wilson (1982:644) stated that "southern range extensions were probably limited to montane boreal regions, with conspicuous gaps in the Great Basin and Great Plains areas." Bailey (1926) categorized the wolverine as an animal of the boreal forests and barrens. Hall (1981) noted historical occurrence in California, Colorado, Idaho, Indiana, Maine, Michigan, Minnesota, Nebraska, New Hampshire, New Mexico, New York, North Dakota, Oregon, Utah, Washington, and Wisconsin. Allen (1942) included Pennsylvania and Vermont along with most of the above states in a detailed discussion of historical occurrence. Schorger (1948) presented further records of wolverines in Wisconsin and Michigan.

The northward diminution of the historical wolverine range apparently began about 1840, the period of extensive exploration, fur trade, and settlement, and of the decline of the northern bison (*Bison bison*) herds. Bailey (1926) described the wolverine as "an animal of the solitudes, shunning human occupation, vanishing with the spread of civilization."

The current North American distribution is considerably reduced but still covers most of Canada, Alaska, and parts of the northwestern conterminous United States (Fig. 2). Only small, isolated wolverine populations occur in eastern Canada (Novak 1975, Prescott 1983), but the species is present over much of the remaining forest area of Canada (Van Zyll de Jong 1975, Kelsall 1981). Most of the Northwest Territories, the Yukon Territory, and Alaska support viable wolverine populations (Manville and Young 1965, Hall 1981, Wilson 1982).

Occasional recent observations have been reported from California, Colorado, Idaho, Nevada, Oregon, Utah, Washington, and Wyoming (Ingram 1973, Yocom 1973, Hornocker 1974, Johnson 1977, Deems and Pursley 1978, Kovach 1981, Hoak et al. 1982, Nead et al. 1984). Some of these areas probably have small viable populations, but the actual status and range remains uncertain. Generally, authentic observations are increasing in some of the more remote areas of the historical range, and numbers are thought to be increasing slowly. Most jurisdictions have protective regulations, and Colorado has started a reintroduction program.

The most viable and widespread population of wolverines within the conterminous 48 states occurs in the Rocky Mountains of Montana. This population, which was near extinction during the early 1900s, recovered through dispersal from Canada and from Glacier National Park in northern Montana (Newby and McDougal 1964). A limited legal harvest is allowed in Montana, which reclassified the wolverine from an unprotected predator to a furbearer in 1976.

LIFE HISTORY

Reproduction

Wolverines are generally solitary animals except during the breeding period. They do not mate for life, and males are seldom associated with females or young during the rearing period (Jackson 1961, Liskop et al. 1981).

Breeding periods vary but generally occur from late spring through early fall. Rausch and Pearson (1972) noted that spermatogenesis commenced during late winter and was active by early spring. Wolverines primarily breed during early summer and carry the dormant, unimplanted blastocyst until the following December or January, when implantation and embryo development begin (Wright and Rausch 1955, Danilov 1965, Pulliainen 1968, Rausch and Pearson 1972). Two Alaskan female carcasses obtained during June had developing follicles in the ovaries and

a third female killed on 24 June had recently conceived (Rausch and Pearson 1972). Magoun and Valkenburg (1983) observed breeding of three pairs of wolverines in northwestern Alaska, two in early June and one in early August. A pair of wolverines were observed during breeding in May 1972 in the Dakota Zoo and the female gave birth 272 days later (Mehrer 1976). Mohr (1938) estimated that the gestation period was 217 days, based on breeding observations at the Copenhagen Zoo. Rausch and Pearson (1972) placed the active gestation period following delayed implantation at 30–40 days. Mead (1981) estimated that delayed implantation lasted 175–230 days and that total gestation took 215–272 days.

Litters are born from February through April. Magoun (1985) reported March litters in arctic Alaska. In the Northwest Territories, litters are probably born during late March and early April (A. Gunn, pers. commun.). Myrberget and Sorumgard (1979) reported that the birth of Scandinavian litters occurred during February and March. Two pregnant females killed in Montana during early March contained fully developed fetuses (Greer et al. 1979). Several litters 2–3 weeks old have been observed in Montana during March (R. Belston, pers. commun.).

Wolverine litters are born in a protected den site frequently associated with an uprooted tree, cave, burrow, overhanging bank, or snow tunnel. Magoun (1985) found that snow tunnels are the most characteristic natal dens used by wolverines in northwestern Alaska. Pulliainen (1968) described 31 den sites found by hunters in Finnish Lapland. Most of these dens (25) were located on the fells (moors); 10 were situated in deep ravines. The remaining 6 dens were found on spruce (*Picea* spp.) and pine (*Pinus* spp.) peat-bogs. All dens had the same general structure—an entrance hole beside a tree or bush, a tunnel in the snow extending to ground level, and lateral tunnels up to 40 m (130 feet) long radiating out at ground level. One of the lateral tunnels contained a shallow, unlined cavity for the young. Dens in Siberia are found in caves, under boulders and tree roots, and in accumulations of woody debris consisting of broken or rotted logs and dry twigs (Stroganov 1969). Similar den sites associated with snow and rocks have been described in Norway (Myrberget 1968) and the Yukon Territory (Youngman 1975). Natal dens of wolverines in Montana are most commonly associated with snow-covered tree roots, logjams, or rocks and boulders (H. Hash, unpubl. data) (Fig. 3).

Wolverine litters may contain from one to five young, but two or three is the usual litter size. Liskop et al. (1981) in British Columbia reported a mean litter size of 2.6 based on five reproductive tracts that had detectable embryos. Rausch and Pearson (1972) reported a mean of 3.5 embryos from an Alaskan–Yukon sample of 54 females. Pulliainen (1968) combined data from seven studies in northern Europe and reported a mean of 2.5 young from 161 litters. Hornocker and Hash (1981) found a mean of 2.2 embryos in a sample of six females from Montana.

Juvenile mortality and poor breeding success apparently contribute to a relatively low reproductive output in wolverine populations. Rausch and Pearson (1972) estimated a ratio of about two kits per adult female in a harvest sample and suggested that this implied an average mortality of 1.5 young per litter during the first summer. Ingles (1965) stated that females produce litters only every second or third year; however, Magoun (1985) reported that females can have litters in successive years. Magoun (1985) observed kits with only 38% of adult females in northwestern Alaska and reported a mean litter size of 1.75 at about 12 weeks old, when kits have abandoned the natal den. Only two of eight mature females monitored during a Montana study were known to produce litters (Hornocker and Hash 1981). Liskop et al. (1981) reported a much higher pregnancy rate for mature females in British Columbia; 23 of 26 females 2 years of age or older were reproductive (the 3 nonreproductive females were estimated to be 6–7 years old). In the same study, all yearlings (N = 16) and 2 of 13 two-year-old females were immature.

Mehrer (1976) described three newborn kits from a captive female as fully covered with fine white fur and having their eyes closed and teeth unerupted. They averaged 84 g (3 ounces) in weight, 12.1 cm (4.8 inches) in crown–rump length (Mehrer's paper gave this as 121 cm, surely a typographical error), and 2.9 cm (1.1 inches) in tail length. Shilo and Tamarovskaya (1981) reported body weights of 84–94 g (3–3.3 ounces), body lengths of 15–16 cm (6–6.3 inches), and tail lengths of 2.6–3.0 cm (1–1.2 inches) for three 1-day-old wolverine kits. Growth and development occurs rapidly (Iversen 1972, Shilo and Tamarovskaya 1981). Kits are weaned at 7–8 weeks, approximately when tooth eruption occurs (Myhre and Myrberget 1975). Young begin to leave the den at 12–14 weeks (Magoun 1985) and often attain weights equal to those of adults by early winter (Rausch and Pearson 1972).

Fig. 3. Location of a wolverine den under a logjam. (Photo: G. Kohler.)

Mortality

Wild wolverines have a variable life expectancy. Jackson (1961) reported longevity in the wild at 8–10 years. Magoun (1985) reported that the tooth cementum age of a wild wolverine was 11 years and that a reproductively active, radio-collared female was 8 years old. Wild wolverines harvested in Montana rarely exceed 8 years of age, with an average of 4–6 years (H. Hash, unpubl. data). Well-cared for captive wolverines often live longer than wild wolverines. Woods (1944) presented records that showed that the average longevity was about 5.5 years and that some animals could live for 15 years. Jackson (1961) believed that captive animals could reach 18 years of age.

ECOLOGY

Habitat

Wolverines occur within a wide variety of habitats consistent with their broad distribution, but primarily occur in boreal forests and tundra areas of the Far North.

The Pacific coastal forest types dominate the wolverine's range along the coast from Washington to British Columbia and southern Alaska for approximately 150 km (93 miles) inland (Bailey 1980). The coastal composition is also present throughout interior Washington and the Idaho panhandle into extreme northwestern Montana. This complex forest type is primarily composed of western white pines (*Pinus monticola*), lodgepole pines (*P. contorta*), ponderosa pines (*P. ponderosa*), grand firs (*Abies grandis*), Douglas-firs (*Pseudotsuga menziesii*), western hemlocks (*Tsuga heterophylla*), Engelmann spruces (*Picea engelmannii*), red cedars (*Thuja plicata*), and western larches (*Larix occidentalis*). Stringers and groves of black cottonwoods (*Populus trichocarpa*) are present along the lower parts of primary drainages. From south to north, and from lower to higher elevations, dominance generally shifts from the pine–fir types to the spruce–alpine types.

The Rocky Mountain forest types dominate the occupied wolverine range in Colorado, Montana, southwestern Alberta, and most of interior British Columbia (Bailey 1980). The primary species are the firs (*Abies* spp.), pines, and larches (*Larix* spp.). Most of the white pines, cedars (*Thuja* spp.), and hemlocks (*Tsuga* spp.)

characteristic of the coastal types are absent. Trembling aspens (*Populus tremuloides*) are common along many slopes and cottonwoods are prevalent along most streams. Many ecotonal areas occur in conjunction with marshes, lakes, cliffs, transition zones between primary cover types, and elevation gradients that appear to be important habitat components. Wolverines prefer marshy areas (Wilson 1982).

The great boreal forest comprises the largest geographic area of occupied wolverine habitat and covers much of Alaska, the southern Northwest Territories, the Yukon Territory, Alberta, and parts of British Columbia (Bailey 1980). Except for the prairie in the southern third of Manitoba and the southwestern corner of Saskatchewan, the wolverine range in Canada is covered by boreal forest types. The black spruce (*Picea mariana*) and white spruce (*P. glauca*) are the dominant species in this type, but balsam firs (*Abies balsamea*), jack pines (*Pinus banksiana*), and tamaracks (*Larix laricina*) are also common in portions of the central and eastern areas. Alpine firs (*Abies lasiocarpa*) and lodgepole pines are present in association with the spruces in the western and northwestern zones. Deciduous species are present in the central and southeastern sections, including the white birch (*Betula papyrifera*), balsam poplar (*Populus balsamifera*), trembling aspen, and a variety of shrubs. This is primarily a lowland forest with an abundance of streams, lakes, and marshes, and it does not have the same ecological variety in terms of vegetative and ecotonal composition as the Rocky Mountain types. Elevational gradients are essentially absent. Much of the northern boreal forest area is remote and has not been significantly influenced by development.

Tundra constitutes the remaining predominant vegetative zone within the northern distribution of the wolverine. Grasses, sedges, lichens, and willow (*Salix* spp.) shrubs primarily constitute the vegetation associated with permafrost. Southward the vegetation changes into birch–lichen woodland, then into boreal forest (Bailey 1980). Species diversity, precipitation, and fertility are low.

Wolverines generally occupy back country or wilderness areas that have little human activity or development. They cross areas of human habitation and development during long-range travels but are only occasionally seen, trapped, or killed in these areas, which are usually fringe zones adjacent to substantial remote habitats. Wolverines usually visit these fringe areas at night. However, occasionally wolverines have been observed scavenging near areas of human occupation (B. Boles, unpubl. rep., Gov. Northwest Territ. Environ. Soc. Program, 1975). Hornocker and Hash (1981) reported that wolverines inhabiting forested areas in Montana appeared reluctant to cross large openings, often skirting the edges or running and loping across in a straight line, in contrast to the meandering travel patterns commonly displayed within timbered areas. Gardner (1985) suggested that rocks may be important cover for wolverines within tundra areas. Rivers, highways, rugged mountain ranges, or other geographic barriers do not appear to limit the travel of wolverines.

Population Density and Dynamics

Reported natural densities of wolverine populations are low compared with those of other carnivores or predators, even under optimal habitat conditions (Quick 1953*a*, Krott 1959, Van Zyll de Jong 1975). Quick (1953*a*) based his estimate of 1 wolverine/207 km^2 (80 miles^2) on returns from a registered Canadian trapline. Hornocker and Hash (1981) estimated that 20 wolverines inhabited a 1,300-km^2 (500 miles^2) study area in northwestern Montana (1 wolverine/65 km^2 [25 miles^2]). Many fringe areas adjacent to the core study area supported wolverines at densities of about 1 wolverine/150–200 km^2 (58–77 miles^2).

Wolverine densities are closely related to the diversity and abundance of food supplies. The wolverine can use a wide range of food resources through its predatory capabilities and its efficiency as a scavenger. Its capacity to cover great distances in relatively short periods, ability to withstand severe cold and to defend a food source against larger predators, keen senses of smell and hearing, a caching instinct, and strong teeth and jaws enable the wolverine to survive as a solitary animal.

Van Zyll de Jong (1975:436) wrote that wolverines remain common where there are large and diverse ungulate populations and that wolverine densities appeared to be directly related to overall biomass and especially to the turnover of large herbivore populations.

Hornocker and Hash (1981) reported that the areas of greatest wolverine densities in Montana supported diverse ungulate populations of elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), moose, mountain goats (*Oreamnos americanus*), and mountain sheep (*Ovis canadensis*). This area also supported large populations of small mammals such as the snowshoe hare (*Lepus americanus*), red squirrel (*Tamiasciurus hudsonicus*), hoary marmot (*Marmota caligata*), and a variety of mice (*Peromyscus* spp.) and voles (*Microtus* spp.). Extremely high densities of Columbian ground squirrels (*Spermophilus columbianus*) were documented within certain habitat types on the study area (Ramirez and Hornocker 1981). Winter activity was primarily centered around occupied areas of big game range. Several efficient predators were present in conjunction with the big game and small mammal populations, including coyotes, mountain lions (*Felis concolor*), lynx (*F. lynx*), bobcats (*F. rufus*), fishers, martens, and badgers (*Taxidea taxus*). Although wolverine attacks on caribou (*Rangifer tarandus*) have been reported (Burkholder 1962), Ognev (1935) and Haglund (1966) reported that wolverines followed more efficient predators to scavenge food.

The greatest numbers of wolverines in North America occur in the Yukon Territory, the Northwest Territories, and Alaska. These remote areas support a variety of big game and small mammal populations as well as a complex of efficient predators. The vast nomadic caribou herds and the high population turnover rates caused by hunting, wolf predation, and natural mortality create an ideal niche for the wolverine.

Sex ratios of wolverines are approximately equal at birth; however, in exploited populations the ratio shifts towards females in the middle to older age-classes. Pulliainen (1968) reported that 15 of 37 kits taken from dens in Finland were females. Rausch and Pearson (1972) found that 8 of 14 fetuses were females. Nine of 19 fetuses recovered from harvested females in Montana were males (D. Palmisciano, pers. commun.). The overall male : female ratio was 1.53:1 for 576 wolverines trapped in Alaska (recalculated from Rausch and Pearson 1972). They also reported ratios of 1.28:1 for kits and 1:1 for animals more than 5 years old. Montana harvest records show about a 2:1 ratio (H. Hash, unpubl. data). Rausch and Pearson (1972) attributed the imbalance in the sex ratio of harvested animals to the males' tendency toward larger home ranges and greater travel than females. Magoun (1985) theorized that in Alaska the disproportionate male harvest resulted partly because fewer male home ranges than female home ranges were available, causing males to remain as transients for longer periods than females; transients travel further with increasing vulnerability to hunting and trapping. She further stated that abundant food resources may influence the proportion of males in the harvest by increasing the number of denning reproductive females, leaving fewer females vulnerable to ground shooting or trapping.

Home Ranges

Home ranges of the wolverine are large, and reports of individual wolverines covering long distances within 1–3 days are common (Krott 1960, Hornocker and Hash 1981, Wilson 1982). Magoun (1985) reported an average yearly home range of 666 km^2 (257 miles^2) for adult males in Alaska, and resident females maintained average summer home ranges of 94 km^2 (36 miles^2). On average, male wolverines were found four times farther from their relocation site of the previous day than were females (Magoun 1985). Whitman et al. (1986) estimated a mean home range of 535 km^2 (207 miles^2) for males (N = 4) and 105 km^2 (41 miles^2) for females (N = 3) in south-central Alaska. Hornocker and Hash (1981) calculated average annual home ranges of 422 km^2 (163 miles^2) and 388 km^2 (150 miles^2) for males and females respectively. One female radiotracked for 2.5 years occu-

pied a total home range of 963 km² (372 miles²), whereas two lactating females used much smaller spring and summer ranges of 100 km² (39 miles²) each (Hornocker and Hash 1981). Thus, home ranges covered by males are considerably larger than those covered by females.

Several factors influence the wolverine's movements and home range size. This species has exceptional stamina for sustained travel over rough terrain and deep snow, and may cover distances up to 65 km (40 miles) without rest if pursued (Wilson 1982). As scavengers, much of the wolverine's travel involves the constant search for carrion. Populations of prey species lose only a small percentage of their total numbers at any given time, and successful predators may have consumed the prey to the point where only limited food remains for the wolverine to scavenge.

The nomadic and migratory nature of many of the big game species that are the wolverine's primary food sources dictates large home ranges and extensive movements for both primary predators and associated wolverines. It is not uncommon for deer and elk to migrate 50–80 km (30–50 miles) from their summer to winter ranges. The nomadic caribou herds of Alaska, the Yukon, and the Northwest Territories travel fairly constantly and their annual movements frequently cover long distances. Wolverines do not closely follow moving game herds on a daily basis, but their overall movements are directly related to food sources.

The daily travel patterns of male wolverines expand during the breeding season. In Montana, males traveled about 30% farther during the spring than during the rest of the year. The movement patterns of male wolverines in Alaska were influenced by breeding behavior from late winter through summer (Magoun 1985).

While finding a suitable home range, young adults of most predatory species commonly exhibit longer and more frequent movements than do older adults. Dispersal phenomena are usually associated with the degree of territoriality displayed by the species. Data show that the dispersal of young adults may contribute to the impression of the use of large home ranges by wolverines (Koehler et al. 1980, Hornocker and Hash 1981). Magoun (1985) specifically noted that dispersal by several young wolverines in Alaska accounted for greater travel distances. However, Gardner et al. (1986) documented a record 378-km (235 miles) movement by an adult male wolverine.

FOOD HABITS

The wolverine is an entirely opportunistic feeder, taking a wide variety of food items depending on their availability within specific locations and habitats. The wolverine is generally a carnivore, but other matter such as fruits, berries (Rausch and Pearson 1972), insects (Krott 1959), and fish (salmonids) (J. Whitman, pers. commun.) may be taken infrequently when more preferred foods are unavailable.

Wolverines tend to cache surplus food items. Ognev (1935) reported as many as 20 foxes and 100 ptarmigans (*Lagopus* spp.) stored under snow and ice. Krott (1960) described the practice of caching food items in detail. Large pieces of carrion may be placed in tree branches. Magoun (1985) also described the caching of arctic ground squirrels (*Spermophilus parryii*), caribou remnants, and a duck in Alaska. Marking with urine, scent, or both occurs at all caches (Wilson 1982).

Wolverines are best described as scavenging predators. They are well adapted for this lifestyle; Haglund (1966) noted that their massive skull structure, powerful jaws, strong teeth, and overall strength enable them to successfully use large bones and frozen meat. The wolverine is strong for its size and can drag large food items several times its own weight over considerable distances to areas of cover and security for the purposes of feeding, caching, or defense. Reports of elk and moose quarters being dragged from hunter kill sites or camps are fairly common. Once a large wolverine takes a prized food item, there are few instances where other animals can successfully interfere. An acute sense of smell enables the wolverine to locate food items under deep snow cover, further increasing its efficiency as a scavenger.

Many authors have recognized the importance of carrion as a primary food source for the wolverine (Teplov 1955, Krott 1959, Pulliamen 1968, Rausch and Pearson 1972, Wilson 1982, Magoun 1985). Analysis of 56 scats collected in Montana showed that deer and elk carrion occurred in 27% of the samples (Hornocker and Hash 1981). Magoun (1985) stated that caribou and arctic ground squirrel carrion were the most important winter foods in northwestern Alaska. Individual wolverines may become skilled at robbing previously captured furbearers and baits from traplines. Reports of robbed cabins and food caches are also common.

The wolverine can kill animals many times its own size, especially when deep snow hinders the prey (Wilson 1982). There are reports of effective predation on North American caribou (Magoun 1985) and European reindeer (*Rangifer tarandus*) (Wilson 1982), and instances of moose being killed by wolverines (Haglund 1966). However, actual first-order predation on large animals probably accounts for a small percentage of the overall wolverine diet except in special situations. Magoun (1985) observed wolverines chasing caribou during summer, but the wolverines were easily outdistanced. Jackson (1961) stated that wolverines run slowly and heavily and can be overtaken by a fast human runner. No instances of predation on moose, deer, or elk were observed during the 5-year Montana study; however, kills of these species made by mountain lions had been used by wolverines.

On the other hand, wolverines are successful predators on a variety of small mammals and birds. Snowshoe hares, grouse, ptarmigan, ground squirrels (*Spermophilus* spp.), tree squirrels (*Sciurus* spp. and *Tamiasciurus* spp.), mice, and voles are important food items. Wolverines in the Mackenzie Valley feed on porcupines (*Erethizon dorsatum*), muskrats (*Ondatra zibethicus*), and fish (Boles, unpubl. rep., 1975). Porcupine quills were found embedded in the chest and forelegs of healthy wolverines in Montana and elsewhere (Rausch and Pearson 1972). Quick (1953*b*) also reported the occurrence of embedded quills. Dead wolverines have been found with their stomachs and digestive tracts impacted with masses of porcupine quills (Grinnell et al. 1937).

Magoun (1985) observed Alaskan wolverines successfully hunting for ground squirrels and for ptarmigans (adults, eggs, and chicks) during spring and summer. Hornocker and Hash (1981) reported that ground squirrels were a primary food source during spring and summer. They also noted that wolverines successfully hunted mice and voles in tree wells formed by deep snow.

BEHAVIOR

The general behavior of the wolverine is comparable with that of other predators, particularly other mustelids. The popular literature has often depicted the wolverine as having a mean disposition and an abnormally ill temper, but most of these observations have apparently been based on wolverines in traps or enclosures. However, under these circumstances, few other animals display the defensive aggression of the wolverine. Wooden and wire live traps will not hold a wolverine, and large-jaw leghold traps frequently fail to hold wolverines.

The wolverine can climb trees, log cabin walls, and rocky cliff or slide areas. It can gnaw, dig, climb, or rip its way into all but the most secure buildings and caches in search of food (Anderson 1929).

Wolverines exhibit extensive marking behavior either by glandular scenting or the biting and scratching of various-size trees (Pulliainen and Ovaskainen 1975, Koehler et al. 1980, Hornocker and Hash 1981, Magoun 1985). Scenting and scratching are frequently combined (Koehler et al. 1980). Buskirk et al. (1986) discussed plantar glands of the feet in North American mustelids, which may serve as an additional scenting and marking mechanism.

Musk, urine, or scats are frequently deposited on trees, rocks, tussocks, logs, or other prominent objects. Jackson (1961) suggested this behavior is used to signal ownership of a food supply. Ewer (1973) thought that anal musk was emitted only during alarm and that marking was performed with the ventral gland. Wolverines have ventral abdominal glands (Fig. 4) similar to

Fig. 4. Howard Hash holding an immobilized wolverine. Note the light-colored patch on the belly that marks the location of the ventral abdominal gland. (Photo: S. Hash.)

those of martens (Hall 1926). However, the ventral glands of the wolverine have not been studied in detail.

The social behavior of wild wolverines resembles that of other solitary, intrasexually territorial carnivores (Powell 1979, Magoun 1985). These animals are primarily solitary except during the breeding season and the spring–fall period associated with the rearing of young. Occasionally, two or more adult wolverines, apparently family members, may travel together during the winter or spring. However, J. Whitman (pers. commun.) argued that during late spring in Alaska adult pairs are probably breeding pairs and not family associations. Observations of wolverines in Montana yielded only one record of two adult wolverines traveling together during winter deep-snow conditions and about 15% of observations described two or more wolverines in summer or fall family groups (H. Hash, unpubl. data). Bee and Hall (1956) reported 17 of 20 observations of solitary animals, 2 of pairs, and 1 of three animals. Wolverines apparently do not engage in any type of cooperative hunting.

Ewer (1973) stated that male wolverines appear to be territorial, excluding other males from their home range but permitting females to enter. Krott (1959) stated that females are mutually intolerant within territories but that more than one female may occur within the typically larger territories of the males. Powell (1979) examined the general spacing patterns of mustelids and found that they used designated intrasexual territories where males are territorial against males and females against females, with extensive territory overlap between sexes. However, Schaller (1972) and Macdonald (1980) pointed out that territoriality is difficult to measure for most carnivores and therefore is, at present, a less useful measure than home range. Magoun (1985) documented the exclusive use of summer home ranges by adult female wolverines in northwestern Alaska. However, data were insufficient to determine if adult male home ranges overlapped; overlap did occur between adult and juvenile males. In south-central Alaska, Gardner (1985) found a varying amount of range overlap between two resident males, between a juvenile and a resident adult, and between a transient adult and a resident adult. The percentage of overlap was least between the adults, irrespective of residential status. Wolverine home ranges frequently overlapped between individuals with unknown residential status of the same and opposite sex in Montana (Hornocker and Hash 1981). The aggressive defense of territories was essentially nonexistent in Montana wolverines; however, extensive scenting and marking behavior appeared to be a social mechanism to maintain individual spacing in time (Koehler et al. 1980). Wolverines, especially adult males, have home ranges that are much too large to actively defend, and regimented territorialism would be detrimental in terms of energy balance to an animal that depends on widespread carrion for much of its food source (Hornocker et al. 1983).

Hornocker and Hash (1981) suggested that a social system that enables greater flexibility of movement to carrion and other food sources would be a more successful strategy for wolverines. They also suggested that high mortality rates contributed to a lack of regimented territorial behavior by eliminating enough animals to impart a "state of flux" (i.e., by removing individuals before they could establish tenure). Similarly, comparatively unexploited populations of Idaho mountain lions showed a highly refined system of territorialism (Hornocker 1969, Seidensticker et al. 1973), whereas individuals in heavily exploited populations were not territorial at all (Hornocker 1976). Gittleman and Harvey (1982) showed that home range size increases with metabolic needs and that carnivores with a large proportion of flesh in their diets have particularly large home ranges.

Wolverines are primarily nocturnal but may be active during daylight hours (Jackson 1961, Wilson 1982). Magoun (1985) noted greater activity during the middle of the long summer days at far northern latitudes in conjunction with ground squirrel activity. Most of the wolverine activity observed during the Montana study occurred at night (Hornocker and Hash 1981). Krott (1960) described a continuous activity cycle comprised of alternating periods of activity and sleep 3–4 hours long that may be disrupted by inclement weather, when more sleeping occurs. Hunger may also disrupt the cycle and cause extended periods of activity. Wolverines are active year-round throughout their range and are nonmigratory.

MANAGEMENT

The wolverine has been heavily exploited by humans throughout much of its holarctic range. The species' unique and valuable fur, its predation (especially on wild and domestic animals in Eurasia), and its raiding of traplines, food caches, camps, and cabins have resulted in virtually unlimited hunting and trapping seasons and even the payment of bounties (Hornocker and Hash 1981). The primary impacts of exploitation in North America apparently occurred from about 1840 to 1925, as manifested by range reductions and extirpation from many areas (Newby and Wright 1955, Jackson 1961, Newby and McDougal 1964, Van Zyll de Jong 1975). Early management-related activities primarily consisted of recording and monitoring the harvest of wolverines by hunters and trappers. Few conservation measures were implemented prior to the 1960s. Totally protective regulations have been adopted by jurisdictions where the species appears to be reoccupying its historical range. However, few jurisdictions have developed specific wolverine management plans or harvest objectives (Munroe and Jackson 1979). Most management decisions regarding seasons and regulations have been based primarily on harvest data, best professional judgement, subjective information, and the results of limited research projects conducted in specific areas.

A general lack of management-oriented information exists largely because wolverine populations are inherently difficult and expensive to study. Densities are relatively low and the wolverine occurs in some of the most inaccessible areas of North

ica. The extremely large home ranges make radiotelemetry cessity in order to maintain reasonable contact with study nals. Aerial monitoring requirements further complicate ch efforts. Wolverine populations seldom warrant high pri- on the agenda of wildlife agencies charged with managing species.

g and Aging Techniques

sexing of wolverines is straightforward because the genitalia oth sexes are apparent on the live animal, carcass, or pelt. methods of assigning sex are primarily based on sexual rphism. Magoun (1985) studied a collection of 535 Alaskan erine skulls and determined that the condylobasal length surement can be used to separate males from females; only a verlap occurred. A successful technique for determining sed on the cross-sectional area of the lower canine teeth has applied to black bears (*Ursus americanus*) by Sauer et al. 6) and to bobcats by Friedrich et al. (1983). This technique robably be successfully used to sex wolverines.

nuli in the cementum of teeth probably provide the most ate means for determining year-class of most mammals son and Taber 1980). Rausch and Pearson (1972) concluded vhile reproductive organs, long bones, and cranial sutures ded an adequate separation of young of the year 10–11 hs of age or less, only cementum deposition provided a reli- estimate of age beyond 1 year. Weight of the baculum was er and less expensive to use than the cementum technique more accurate than the long bone–cranial ossification tech- e. However, Rausch and Pearson (1972) believed that mate- for this method would be no easier to obtain than for the entum annuli method. Dry lens weight was judged unsuit- for determining age (Rausch and Pearson 1972). D. Palmis- (pers. commun.) determined that annuli in wolverine ines are readable to an age of 6–8 years, beyond which annuli ome generally indistinct. Johnston and Watt (1981) described ect method of obtaining annuli counts from undecalcified, ined sections of carnivore canine teeth that can probably be lied to wolverines. D. Palmisciano (pers. commun.) applied foramen diameter method described by Crowe (1972) for ats to a sample of Montana wolverine teeth previously aged nuli counts and determined that the ratio of the overall n diameter to the inside diameter of the longitudinal pulp al gives a valid year-class up to age three. Whitman et al. (1986) body weight, overall condition of teeth, general physical ition, and physiological signs of aging as criteria to classify nobilized live animals or carcasses as juveniles, young adults, lts, or old adults. Magoun (1985) estimated the ages of live- ped wolverines using several criteria: extracted tooth cemen- annuli, general condition of teeth, length of teats for ales, length of testes for males, extent of scarring and wounds, l observations of breeding. Based on the time of year that cap- occurred, wolverines were categorized as adults, subadults, veniles. Similar factors were used to categorize 24 animals ied in Montana; extensive tooth wear and breakage were gen- lly evident in what appeared to be old adults (Hornocker and h 1981).

nsusing and Estimating Population Numbers

st conventional methods that have been successfully used to ss population numbers of furbearers present difficulties n applied to the wolverine. Actual counts, sample counts, and nsect counts are essentially precluded by naturally low densi- s, reclusive and nocturnal habits, habitation of remote and sted areas, and widespread distribution. Various mark– pture methods would require an impractical trapping effort capture a valid sample because of low densities, low capture cess, and logistical constraints.

he most satisfactory estimates of wolverine population num- have been obtained in conjunction with extensive radiotele- try research projects. Home range size and degree of clusivity, population structure, and mark–recapture data were used to derive estimates of population numbers. Based on an average female summer range of 94 km² (36 miles²), a male home range of 625 km² (241 miles²), and a reproductive rate of 0.6 kits/year/female, Magoun (1985) calculated a resident fall population of 821 wolverines for a specific management unit in Alaska. Hornocker and Hash (1981) combined data from radio-tracking, mark–recapture, and snowtracking to estimate a minimum population of 20 wolverines on their 1,300-km² (502 miles²) study area, a density of one animal/65 km² (25 miles²). Satisfactory estimates of wolverine numbers could probably be derived by carefully extrapolating density values to other areas with similar habitat, food resources, harvest pressure and yield, and general predator–prey ecology. Extrapolation would be greatly enhanced by companion indices such as track counts or bait-station surveys.

A procedure for estimating harvest rate and associated population size, which uses data on differential harvest by sex- and age categories as well as information on accumulated harvest effort, has been described by Fraser (1976), Paloheimo and Fraser (1981), and Fraser et al. (1982). The method considers the progressive decline of males relative to females because of unequal harvest vulnerability of the sexes in population cohorts with initial sex ratios of 1:1. The fundamental assumption supporting this technique is that harvest changes sex ratios with age; however, initially balanced sex ratios and nonharvest mortality are also assumed. Since disproportionate harvests distinctly occur in wolverine populations (Rausch and Pearson 1972, Hornocker and Hash 1981, Magoun 1985), this method can probably be applied to wolverines successfully. Fraser et al. (1982) cautioned that changes in harvest methods or timing affect the differential vulnerability of the sexes and the validity of the estimation method.

Golden (1986) conducted aerial furbearer track counts in Alaska. Because wolverine tracks and trails are distinctive, aerial surveys can probably be applied to unforested northern areas to obtain estimates of wolverine numbers. However, Hornocker and Hash (1981:1300) stated: "Regional, rather than local, populations must be considered in any management program.... By traveling widely in a short period of time, individual wolverines give a false impression of abundance. Tracks encountered in widely separated major drainages, often divided by high mountain ranges, may in fact be made by the same individual. This should be taken into account when unit or area harvest regulations are set."

Estimating Population Growth

Valid estimates of changing population numbers for most wildlife species are best derived by several complementary techniques that assess fecundity and mortality, and which serve to check and improve final results. Although few of the various methods used to successfully monitor population growth in furbearer populations have been applied to wolverines, some of the techniques may be practically applied to this species with little or no modification.

Widespread and long-term radiotelemetry investigations can yield excellent information on survival, density, and reproduction (Hornocker and Hash 1981, Magoun 1985); however, inherent economic and logistical constraints render them largely impractical as a management tool for the sustained assessment of wolverine population parameters.

The most reliable information on fecundity is obtained from the analysis of female reproductive tracts acquired from harvested animals. The tracts can be examined for corpora lutea and placental scars (Wright and Rausch 1955, Greer and Palmisciano 1982, Magoun 1985). Placental scars persist for 1 year or more but become progressively less distinct following birth, and bleaching and clearing techniques may be required (Wright and Rausch 1955). Counts of corpora lutea accurately reveal the number of ripe ova or eggs released from the ovary during estrus, which translates into an estimate of litter size at birth. Counts of placental scars combined with counts of corpora lutea provide a more reliable estimate of fecundity (Johnson and Holloran 1985) particularly for wolverines, which may not produce litters every year

(Ingles 1965, Hornocker and Hash 1981). Recruitment can be estimated by applying quantitative survival data to basic fecundity measures. Magoun (1985) obtained survival rates of 1.75 kits per litter by directly observing radiotagged females.

Indirect indices provide more feasible means of monitoring changes in population levels. A modification of the scent-station survey (Linhart and Knowlton 1975, Roughton 1982, Roughton and Sweeny 1982, Conner et al. 1983) conducted under snowtracking conditions is suitable for wolverines, which readily visit winter bait stations. A linear transect of bait stations located at intervals of 15–20 km (9–12 miles) will reduce the possibility of several stations being visited by one animal. This method will yield an index of the relative abundance of wolverines over time. The number of stations per transect and the number of days over which each transect is visited can be varied to determine the most efficient sampling procedure (Roughton and Sweeny 1982).

Depending on snow cover conditions, systematic track counts (Fig. 5) may also provide information on the relative abundance of wolverines (Mauer 1985). Zezulak (1980) reported that track-count transects conducted after fresh snow may depict changes in bobcat population levels more accurately than scent-station surveys. However, wolverines appear to be much more responsive to bait or scent than bobcats; as a result, bait stations may be more useful. Population data on primary food-source species should also be collected in conjunction with bait-station or track-count surveys.

Furbearer population trend indices are frequently maintained by monitoring harvest level and harvest effort data through pelt tagging or sealing, trapper mail questionnaires, fur dealer transactions, or trapper reports. Because the total wolverine harvest is comparatively small, this method should be quite feasible.

Knowledge of the wolverine is likely inadequate to enable realistic computer population modeling as applied to many other species. However, this method will become more applicable as data bases and knowledge of the species increase.

Regulating the Harvest

Wolverine harvest levels are difficult to closely control; however, harvest rates have remained relatively stable. The incidental take of this species in traps primarily intended for other species accounts for part of the harvest. Wolverines are difficult to release in good condition without special equipment and some are lost through unintentional captures. The wolverine is also hunted as a game animal throughout parts of its range. Harvest and incidental losses are difficult to document because of processing delays and possible poor compliance with tagging regulations (as reported in Alaska by Magoun 1985).

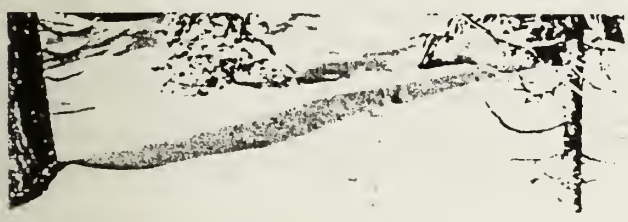

Fig. 5. Track of a wolverine in fresh snow. (Photo: H. Hash.)

Furbearer harvests are regulated by the duration and timing of open seasons, individual trapper limits, and geographic harvest quotas. Pelt tagging or registration is needed to provide current knowledge of numbers harvested. Alaska requires that all wolverine pelts taken by trapping be sealed within 30 days following the closure of the trapping season and that those taken by hunting be sealed within 60 days (Hinman and Kramer 1986). All wolverine pelts taken in Montana must be tagged within 10 days after season closure. Erickson (1982) suggested that rigorously enforced pelt registration programs were particularly applicable to species with small total harvests.

There are insufficient data to properly evaluate whether populations in most jurisdictions can sustain present harvest levels; however, in Alaska, an apparent decline in the wolverine harvest has occurred from 1971–72 to the present (J. Whitman, unpubl. rep., Alaska Dep. Fish and Game, 1984). Whitman recommended that the trapping season be reduced to enable populations to recover.

Live Capture Methods

The wolverine is a difficult animal to capture and handle humanely without special equipment. A system combining sturdy live traps, a portable squeeze chute, and prompt immobilization with aqueous ketamine hydrochloride (Ketalar) has been successfully used (Hash and Hornocker 1980). Animals were captured in live traps with a sliding dropdoor and weatherproof trigger mechanism. Traps were baited with approximately 1 kg (2 pounds) of fresh meat, and a visual attractor (a piece of cloth) was suspended from a branch or pole near the set. On capture a portable squeeze chute made from metal mesh with a movable top section was attached to mounting lugs adjacent to the trap door. The chute was covered with canvas to darken the interior and the trap door was raised to enable the animal to move into the chute. The door and the moveable top section of the squeeze chute were then lowered, forcing the animal to the floor until drugs could be administered with a jabstick or syringe. Immobilization usually occurred within 5 min, recovery began within about 45 min, and full recovery required 3–8 hours (Hash and Hornocker 1980).

Wolverines were immobilized with dosages of Ketalar that ranged from 17.2 to 25.5 mg/kg body weight (Hash and Hornocker 1980). Generally, dosages of less than 16 mg/kg did not produce adequate periods of immobilization and dosages of more than 25 mg/kg induced immobilization beyond that required for normal research or transport purposes. Muscle relaxants as described by Ramsden et al. (1976) or general tranquilizers such as xylazine (Rompun) might be carefully combined with Ketalar to reduce muscle rigidity. Moderate muscle rigidity and excessive salivation were noted in all animals, necessitating the maintenance of an adequate airway. Wolverines were positioned to facilitate the gravitational flow of saliva to prevent aspiration. Anesthetized animals were particularly susceptible to sudden tactile stimulation, so all were handled as gently as possible. Each immobilized animal received 2 ml bicillin (Wyeth) prophylactically, and no animal deaths were attributable to the effects of immobilization.

Wolverines have been immobilized with ketamine (Hash and Hornocker 1980), a combination of phencyclidine and promazine (Seal and Erickson 1969, Seal et al. 1970), and a combination of etorphine and xylazine (Ballard et al. 1982).

Immobilized animals should not be released until fully recovered, as they are susceptible to predation and accidents (Fig. 6). Drugged animals were removed from the chute for processing and dilated eyes were covered with a dark cloth to prevent damage and reduce sight responses.

Fig. 6. Fully recovered wolverine released from a live trap after handling. (Photo: H. Hash.)

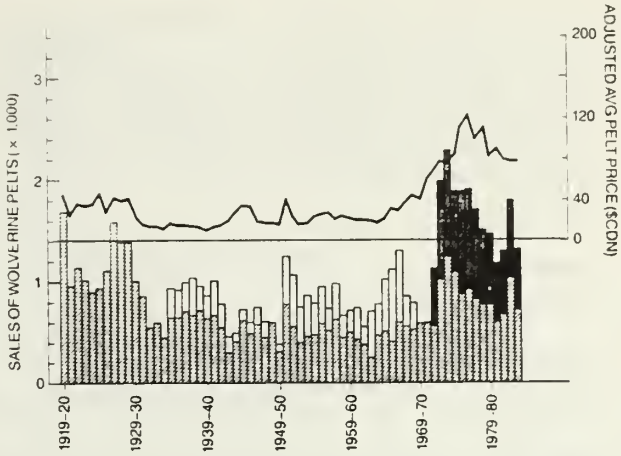

Fig. 7. Sales of wolverine pelts in Canada (hatched bars) and the United States (pre-1970, open bars; post-1970, stippled bars). Solid line shows adjusted average price (1970 $CDN = 1.0). Source: Obbard et al. (1987).

Wolverines that will not enter a live trap may be captured using a conventional leghold trap with padded or offset jaws. A typical cubby or bait set may be prepared in conjunction with a radiotelemetry transmitter connected to the trap chain so that the event of capture is known immediately. It is essential to immobilize and remove the animal from the trap as soon as possible to prevent damage to the foot, leg, and teeth.

Whitman and Ballard (1984) and Magoun (1985) successfully captured wolverines with cagelike live traps, by using a dart gun from a helicopter or snowmobile, and by darting animals in caves or snow tunnels. It is possible to capture litters by digging out the den site (Pulliainen 1968; R. Belston, C. Garland, H. Kitchens, pers. commun.). This is an arduous task and is not always successful because of rocks or other obstructions.

The use of specially selected and trained trailhounds may be useful for the capture and handling of wild wolverines, much as they are commonly used to capture mountain lions. Jackson (1954) stated that the wolverine is easily treed by a barking dog, yet when cornered will outfight any dog. Animals pursued this way will climb a tree or stop in some protected site and thus may be immobilized with a dart gun. C. Garland (pers. commun.) treed a Montana wolverine in deep snow conditions with trailhounds. This capture method has not been widely practised and further development is required.

Economic Importance

The wolverine is not an economically important furbearer on the international market; however, pelts are often valued beyond sale or barter in many local communities of the Far North, especially among Eskimos and Athabascan Indians. Recent North American harvests in the 1980s have been approximately 1,200–1,800 animals annually (Fig. 7). From 1973–74 to 1981–82 the average price of wolverine pelts was exceeded only by brown bear (*Ursus arctos*), polar bear (*U. maritimus*), and lynx pelts, and occasionally by mountain lion pelts. However, because of low numbers, the total value of the wolverine harvest is smaller than that of many furbearers (Obbard et al. 1987). The average price of wolverine pelts has risen greatly since the early 1960s (Fig. 7). Wolverine fur is primarily used by local and native enterprises for parka ruffs and trim for outer garments. It has not been widely sought for fashion garments by the international fur industry, but the full pelt of the wolverine is highly valued as a trophy when processed into a rug or mount.

Despite a reputation for being a nuisance animal, the wolverine cannot represent any serious conflict with human interests, except on rare occasions. Its overall natural low densities and remote distribution provide limited opportunities for significant conflicts, except for some areas in Alaska and possibly Canada. The occasional incident is rarely serious and can best be handled on a local basis.

CONCLUSIONS

Recent research and field studies have improved our understanding of the wolverine. Although considerable progress has been made, further work is needed to test and develop reliable and practical density indicators. Status and occurrence verification programs should be implemented by jurisdictions where wolverines are reported or suspected. There are many areas where the range is uncertain, but general reports (Hornocker 1974, Novak 1975, Johnson 1977, Kovach 1981, Hoak et al. 1982, Nead et al. 1984) have indicated reoccupancy of some parts of its historical range where suitable habitat occurs.

Hunting and trapping appear to be the primary sources of mortality for adult wolverines, as the species has few natural enemies. Wolverines are vulnerable to bait trapping because their scavenging nature and long-distance travel patterns increase the overall probability of their encountering traps, even in remote areas. In contrast, females with newborn young are limited in their ranging and foraging and as a result become especially vulnerable to easily obtained trap baits (Hornocker and Hash 1981). Bait trapping for all species should be prohibited in areas where expansion of wolverine populations is desired. Harvest seasons should be closed during late winter and early spring (Feb–Apr) to protect females with kits. Wolverines are susceptible to traps intended for other species; any set made for a coyote, lynx, bobcat, or wolf can effectively take a wolverine.

Much of the general wolverine population decline and extirpation that occurred during the late 1800s and early 1900s on many ranges, particularly the conterminous United States, has been attributed to overtrapping and habitat degradation. It is essential that the harvest of a species with a naturally low density and relatively low reproductive potential be monitored closely. Any actual or contemplated harvest program should be directed only towards viable populations that are producing surplus animals. General populations or localized subpopulations that are expanding their ranges or that are in the process of reestablishment should be fully protected. Areas of the wolverine's historical range with suitable habitat which are currently vacant or only occasionally occupied would be ideally suited to reintroduction programs. Healthy wild wolverines should be released at a ratio of two or four females per male, which would facilitate the restoration of this species in areas that can support viable wild populations.

The future of the wolverine appears bright. The species has survived the pioneer periods of unregulated trapping, hunting,

and predator control, accelerated and irresponsible natural resource development, and widespread habitat degradation. The designation of vast national park and wilderness areas has greatly benefited the wolverine. Our greater awareness and responsibility toward environmental issues and threatened species will favor the survival of the wolverine, as well as many other wildlife species. Carefully regulated harvest programs, the implementation of refined monitoring techniques, appropriate reintroduction programs, and the preservation of adequate suitable habitat should ensure the survival of the wolverine for future generations.

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IMMOBILIZING WOLVERINES WITH KETAMINE HYDROCHLORIDE

Little information on capture or handling techniques for wolverines (*Gulo gulo*) is available. The development of a safe immobilization procedure was essential to the success of a study of this aggressive species.

Other researchers have used ketamine hydrochloride to achieve various planes of anesthesia in several wildlife species (Dolensek 1971, Bigler and Hoff 1974, Haupert and Lindeen 1974). Ramsden et al. (1976) reported successful use of this drug on mink (*Mustela vison*).

METHODS AND MATERIALS

Wolverines were captured in barrel-type traps on a 4,900-km^2 study area primarily composed of the South Fork of the Flathead River Drainage in northwestern Montana. All animals were captured and processed during deep-snow field conditions from early 1974 through April 1977.

Aqueous ketamine hydrochloride ("Ketalar"; Parke, Davis & Co.) is a quick-acting drug. Collins (1976) described its action as producing a peculiar state of unconsciousness in which the patient appears not to be asleep or anesthetized, but rather "disconnected" from his surroundings. Pharmacologic studies in man support the observation in laboratory animals that the anesthetic effect of ketamine is highly selective. Association pathways in the brain apparently are blocked first. The drug affects the neocorticothalamic system intensively, followed by obtundation of the reticular-activating and limbic systems. Ketamine seems capable of stimulating some areas (medulla and limbic system) of the brain while simultaneously depressing another (cortex). These changes were interpreted to represent depression of the thalamoneocortical system and concurrent activation of the limbic system; therefore, functional dissociation of the 2 brain areas results.

Ketalar (100 mg/ml) was administered by intramuscular injection into the hip area. A rigid jabstick in conjunction with 3.0-ml syringes and 18-gauge, 2.5-cm-long stainless-steel needles was used for drug delivery. All animals were administered 2 ml of bicillin (Wyeth) prophylactically.

Captured animals were transferred from barrel traps to a connectable squeeze chute. Animals entered the chute more readily from the trap if the interior was darkened with an opaque cover. Upon entry, the cover was removed and the mobile top lowered and secured to restrain the wolverine. The animal's weight was estimated and the calculated dosage administered promptly. Once immobilized, all animals were

Table 1. Immobilization effects of ketamine hydrochloride on wolverines in Montana, 1974–77

Sex	Body weight (kg)	Drug dosage (mg)	Dosage/body wt (mg/kg)	Response interval (min)			
				1st effects	Onset of immobilization	Immobilization	Recovery
Male	10.89	230	21.12	2	3	36	30
	10.89	250	22.96	2	3	42	35
	11.34	250	22.05	2	5	33	40
	11.79	250	21.20	3	5	20	30
	11.79	250	21.20	2	3	22	30
	13.60	240	17.65	3	5	20	18
	13.60	300	22.06	3	5	36	28
	14.52	250	17.22	2	4	18	16
$\bar{x}$	12.30	252.5	20.68	2.12	4.12	28.40	28.37
Female	6.35	150	23.62	4	6	61	75
	6.80	140	20.59	1	3	62	40
	7.23	160	22.13	2	3	35	40
	7.26	130	17.91	2	4	26	15
	7.26	150	20.66	2	5	40	71
	7.26	150	20.66	4	5	30	32
	7.26	160	22.04	1	3	51	40
	7.26	160	22.04	2	5	50	35
	7.26	160	22.04	1	3	55	60
	7.26	160	22.04	3	4	34	24
	7.71	160	20.75	3	4	47	40
	7.71	160	20.75	2	3	45	60
	7.71	200	25.94	2	4	47	70
	8.16	190	23.28	1	3	68	80
	8.62	180	20.88	2	5	42	45
	8.62	220	25.52	3	4	39	61
	9.07	200	22.05	1	3	27	20
	9.53	200	20.99	1	2	38	25
$\bar{x}$	7.68	168.33	21.88	2.05	3.83	44.28	46.28

weighed accurately. All wolverines were held in a portable enclosure until complete recovery had occurred before being released. Full recovery required 3–8 hours.

RESULTS AND DISCUSSION

Fifteen wolverines were each immobilized once, 1 female 7 times, and 1 male twice, for a total of 24 immobilizations of 17 animals (Table 1). The 1st-effects interval was measured from the time of injection until aggression diminished. The onset of immobility is the total time until the animal can be handled safely. Immobility is the period when handling is safe, and is terminated by increasing activity and signs of aggression. The recovery period begins with termination of the safe-handling period and ends when all faculties apparently are regained.

Considering comparable estimated mean dosages, the initial effects and onset of immobility intervals were relatively constant among all individuals. Mean duration of immobility and recovery intervals of individuals of like sexes were comparable (Table 1). Male wolverines exhibited shorter periods of safe handling with a mean anesthesia index (Index = mean mobility interval/mean dosage [mg/kg]) of 1.37 minutes/ml compared to a value of 2.02 minutes/ml for females.

The higher dosages intensified inactivation and extended all intervals without detectable clinical responses. Immobilized wolverines displayed nystagmus and pupil dilation. The eyes were covered with a dark cloth to prevent eye damage from sunlight or to prevent the animal from responding to the sight of researchers.

Wolverines were immobilized successfully with varying dosages of Ketalar that ranged from 17.22 to 25.52 mg/kg body weight (Table 1). Generally, dosages below 16.00 mg/kg did not produce adequate periods of immobility. Dosages above 25.00 mg/kg induced immobilization extending beyond that required for investigational procedures. If surgical-plane anesthesia is required, dosages somewhat above the maxima for each sex in Table 1 are indicated. Muscle relaxants as described by Ramsden et al. (1976) might be combined carefully with Ketalar to overcome muscle rigidity. An adequate airway must be maintained.

The 1st apparent effects of Ketalar on wolverines are a brief excitation period followed by loss of aggression and coordination. The reaction progresses to an apparent state of catalepsy in which the animal is unconscious, but still responds to painful stimuli. Laryngeal and pharyngeal reflexes are unimpaired. Moderate muscle rigidity and excessive salivation were noted in all animals. Wolverines were positioned to facilitate gravity flow of saliva and to avoid aspiration. Anesthesized animals were particularly susceptible to sudden tactile stimulation, and repeated stimulation produced muscle spasm. All animals were handled as gently as possible.

No wolverine died as a result of administering Ketalar, and the drug produced satisfactory results with no apparent ill effects.

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Ecology of the wolverine in northwestern Montana

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HORNOCKER, M. G., and H. S. HASH. 1981. Ecology of the wolverine in northwestern Montana. Can. J. Zool. 59: 1286–1301

A population of wolverines was studied in northwestern Montana for 5 years (1972–1977). Twenty-four wolverines were captured in live traps, individually marked, and released. Ten individuals were recaptured 74 times. Twenty wolverines were fitted with radio transmitters and 576 relocations were made over a 4-year period. A minimum population size of 20 was estimated for the 1300-km^2 area, or one wolverine per 65 km^2. The population was believed stable. This stability was maintained by mortality and dispersal. Wolverines utilized relatively large areas. The size and shape of ranges were not affected by rivers, reservoirs, highways, or major mountain ranges. The average yearly range of male and female wolverines was 422 and 388 km^2, respectively. Wolverines exhibited fidelity to a given area, but several individuals of both sexes made frequent long movements to other areas. In all instances wolverines returned to the same area. Ranges overlapped between individuals of the same and opposite sex. Territorial defense was essentially nonexisent. Wolverines scent marked to maintain spacing in time but not area. Wolverines appeared to select *Abies* cover types throughout the year; this selection was strongest in summer. In Montana, wilderness habitat coupled with more restrictive harvest regulations should provide for secure wolverine populations in the foreseeable future.

HORNOCKER, M. G., et H. S. HASH. 1981. Ecology of the wolverine in northwestern Montana. Can. J. Zool. 59: 1286–1301.

Une population de gloutons a été étudiée durant 5 ans (1972–1977) dans le nord-ouest de Montana. Vingt-quatre gloutons ont été capturés, marqués et relâchés. Dix de ces individus ont été capturés 74 fois. Vingt gloutons ont été munis d'émetteurs-radio et ont pu ête relocalisés 576 fois au cours d'une période de 4 ans. La population minimale a été estimée à 20 gloutons dans l'aire de 1300 km^2, soit 1 glouton par 65 km^2. La population semble stable et cette stabilité est assurée par la mortalité et la dispersion. Les gloutons utilisent des aires relativement étendues. Les dimensions et la forme des aires vitales ne sont affectées ni par les cours d'eau, ni par les réservoirs, ni par les routes, ni par la présence de chaines de montagnes importantes. L'aire vitale annuelle moyenne d'un mâle est de 42.2 km^2 et celle d'une femelles de 388 km^2. Les gloutons sont fidèles à une aire donnée, mais plusieurs individus des deux sexes font souvent des incursions de longue durée dans d'autres régions. Les gloutons retournent toujours à la même aire. Les aires vitales de plusieurs individus du même sexe ou de sexes opposés se chevauchent. Les gloutons ne font aucune défense de territoire. Les gloutons font des marques de substance odorante pour assurer l'espacement dans le temps et non dans l'espace. Ils semblent préférer les couvertures de type *Abies* durant toute l'année, mais cette sélection se manifeste surtout durant l'été. Dans le Montana, les habitats sauvages actuels combinés à des lois plus strictes sur les captures devraient assurer la survie des populations de gloutons durant les années à venir.

[Traduit par le journal]

Introduction and background

Little is known of the population ecology of the largest terrestrial mustelid (*Gulo gulo*). Although the species has a vast circumpolar range, few scientists have attempted to study wolverines in their natural habitat. Van Zyll de Jong (1975) states that the reason for this is due to the species being uncommon, highly mobile, and restricted to the more remote and inaccessible parts of the country. Some studies, mainly utilizing snow tracking, have been carried out in Europe (Teplov 1955, cited by Heptner and Nasimovitch 1967; Haglund 1966; Pulliainen 1968; Myrberget 1970). Krott (1959) studied semitame wolverines in Sweden. Most wolverine studies in North America have dealt with the species' breeding biology and other information gained from carcasses (Wright and Rausch 1955; Kurten and Rausch 1959; Wright 1963; Fausch and Pearson 1972).

Authors of recent papers dealing with the wolverines' status and distribution all have pointed out the dearth of information in the literature (Nowak 1973; Dagg and Campbell 1974; United States Fish and Wildlife Service 1974; van Zyll de Jong 1975). All urge the inception of ecological research. Dagg and Campbell (1974) state "almost nothing is known about the density of wolverine populations in North America or about their exact distribution." They recommend extensive research be initiated "on wolverines in their native habitat. Radiotelemetric tracking should enable biologists to determine the territorial needs of individuals. . . ."

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Clearly there was need for intensive research on this species. Our research, carried out from 1973 to 1978, was designed to study a free-ranging population of wolverines by observing marked individuals. General objectives were to (1) investigate the dynamics of a wolverine population and (2) to determine movement, range, and habitat use of marked wolverines.

Study area

Wolverines occur in several northwestern states but only Montana has adequate numbers to constitute viable populations. Newby and Wright (1955) stated that wolverine populations in Montana were near extinction by 1920. However, numbers have increased in the western, mountainous region of the state in the past 30 years (Newby and Wright 1955; Newby and McDougal 1964). The northwestern region of Montana therefore appeared to offer the greatest potential for studying wolverines in the contiguous 48 United States.

The study area (Fig. 1) consisted primarily of the South Fork of the Flathead drainage, and secondarily portions of the Sun, Swan, and Middle Fork of the Flathead drainages. This area makes up about 1300 km^2 of the Flathead National Forest. About one-half the study area is remote, primarily used for logging and recreational purposes; the other, the Bob Marshall Wilderness Area, is managed as bona fide wilderness. Topography and vegetation are practically identical in both areas and the percentage of different vegetative types, considering topographical features, is the same.

The study area is characterized by rugged topography. Sharp ridges and deep U-shaped valleys generally lie in a north–south direction. The numerous, major side drainages are dendritic and often drain small cirque-contained mountain lakes. Evidence of glaciation is apparent down to about 1300 m above sea level.

Elevations vary uniformly along the South Fork from 1085 m at Hungry Horse Reservoir to 1387 m at Big Prairie, 145 km south. Ridge elevations vary from 1799 m above sea level at Columbia Mountain to 4374 m at Swan Peak; however, most of the high terrain lies between 1982 and 2439 m. Most slopes rise abruptly, producing gradients between 30 and 65%.

The general climate is affected by predominately westerly winds and the Mission and Swan ranges. Moisture laden, coastal winds produce variable amounts of precipitation from September through June. Approximately 60% of the moisture falls as snow from October through March. Annual rainfall at Spotted Bear has averaged 77.7 cm for the last 10 years with an average January snow depth of 116.8 cm (United States Department of Agriculture Forest Service weather records). Continental rather than coastal climatic factors influence the summer conditions. Summer precipitation, cloud cover, and humidity are usually low, and combine to create wildfire conditions.

The vegetation on the study area generally conforms to major habitat and cover types with variations and ecotones. This phenomenon produces irregular and indistinct boundaries between vegetative zones. Habeck (1972) found a similar effect widespread in the Selway–Bitterroot Wilderness of Montana and Idaho.

The vegetative types have been described by Pfister et al. (1977). Limited areas of the *Pinus ponderosa* series are found primarily along major drainages on the lower elevations of south and west lower slopes. The upper South Fork areas contain the *Pinus ponderosa – Agropyron spicatum* habitat type whereas *Symphoricarpos albus* is the dominate understory in the pine stands along the Swan Valley.

Pseudotsuga menziesii – Agropyron spicatum or *Pseudotsuga menziesii – Symphoricarpos* spp. are the habitat types on the southerly and westerly slopes. These habitat types are widespread, making up the bulk of the big game winter ranges in the area. *Pinus ponderosa*, *Larix occidentalis*, and *Pinus contorta* are common seral species.

Limited areas of *Picea* spp. – *Clintonia uniflora*, *Galium triflorum*, and *Linnaea borealis* are present in low to midelevation moist sites. *Pseudotsuga menziesii*, *Pinus contorta*, and *Larix occidentalis* again are common seral species. *Populus nigra* is present in many of the bottomland, mesic sites.

The *Abies lasiocarpa* series are the most widely distributed habitat types on the area. *Abies lasiocarpa – Clintonia* spp. are dominant along drainage bottoms and lower slopes. *Abies lasiocarpa – Xerophillum tenax*, *Luzula hitchcockii*, *Pinus albicaulis*, or *Vaccinium globulare* types are commonly found on the higher ridge tops and medium to upper slopes. *Abies lasiocarpa – Menziesia ferruginea*, *Alnus sinuata*, and *Vaccinium scoparium* constitute most of the moist high elevation areas on north and easterly aspects. *Abies grandis*, *Larix occidentalis*, *Pinus contorta*, and *Populus nigra* are the primary seral species.

Wildfires have removed the climax coniferous forests from some areas which are presently forested stands of seral or intermediate species; however, representative climax stands are present in many areas.

Many clear-cut logging areas are present in the non-wilderness portion of the study area. These range from recently logged and sparsely vegetated to fully stocked with shrub and (or) conifer reproduction on the older stands that were logged approximately 15 years ago.

Materials and methods

Capture, marking, snow tracking, and radio telemetry were the primary methods used to gather data on wolverines. Inten-

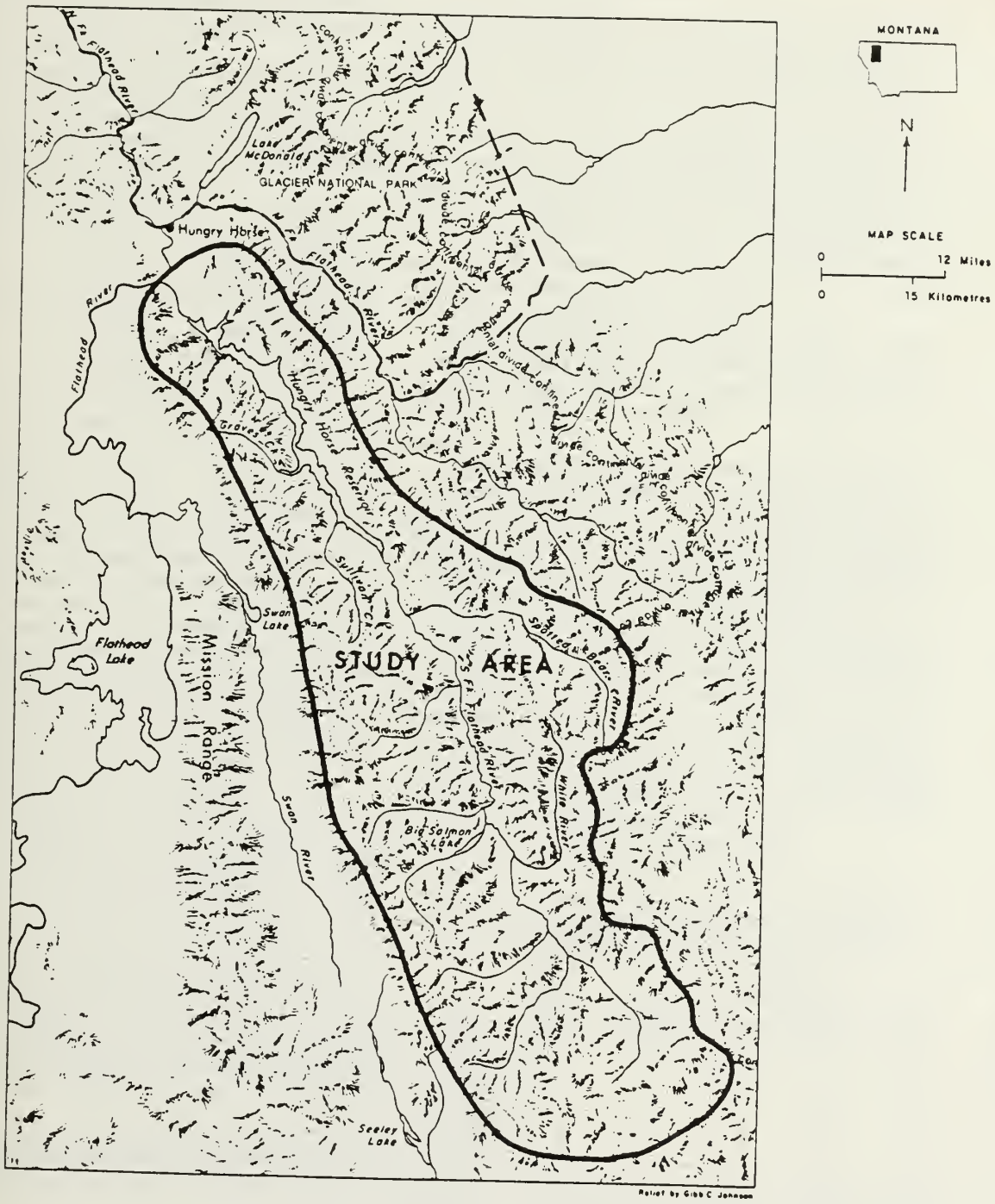

FIG. 1. The study area in northwestern Montana.

sive trapping efforts were conducted continuously from the 1st of December to April 15 each year from 1972 to 1977. The study area was open to commercial trapping during the winters of 1972–1973 and 1973–1974. At our request, the Montana Fish and Game Commission closed the entire South Fork drainage to commercial trapping during the last three winters of the study.

Sixty-six live traps of three types were used: wooden box type, wire mesh box type, and 159-L steel drum traps. Each had a single, sliding steel door. A "squeeze chute" made of

steel mesh was constructed to attach to the wooden and barrel traps. This facilitated the drugging and handling of captured wolverines. Traps were selectively distributed along approximately 122 km of roads and (or) trails that generally followed the river or major tributaries.

Road-killed deer provided by the Montana Fish and Game Department and horse meat were used for bait. A piece of meat was hung near, as well as inside, the live trap. All traps were checked daily when a wolverine was know to be in the area and regularly within each 48-h period.

Two separate traplines were operated each season. A lower line 29 km around both sides of Hungry Horse Reservoir consisted of 18 live traps placed in major side drainages. This area has been logged more intensively and is more accessible than other areas trapped. An upper line in the Spotted Bear area consisted of 28 traps along 50 km of roads.

A third trapline 40 km long using 20 live traps was operated for the 1975–1976 and 1976–1977 seasons in the Bob Marshall Wilderness Area. This effort was initiated to maintain contact with individual animals captured outside the wilderness area which radio tracking showed were ranging deep into the wilderness. It also enabled us to compare wolverine population density, range, and habitat use within wilderness habitat with that in an area managed for multiple use.

Captured wolverines were immobilized with ketamine hydrochloride (Hash and Hornocker 1980), weighed, measured, lip tattooed, and tagged with numbered 15-mm plastic ear tags.

Radio transmitters were placed on all wolverines captured after April 1973 and radio telemetry was the major technique utilized to collect data on movement, range, and habitat utilization. The transmitters, in the 164-MHz range, were fitted inside flexible collars. The instrumented animals were monitored primarily by fixed-wing aircraft equipped with a yagi antenna on each wing strut. Normally, two flights a week were flown, weather permitting. If a wolverine exhibited unusual movement, additional flights were made. A grid system based on the standard Universal Transverse Mercator, was constructed and all relocation data were coded to fit this system. A total of 460.5 h of aerial radio tracking was recorded. Animals also were monitored by ground radio tracking. Seasonal and yearly range indices were delineated using the minimum polygon method (Stickel 1954; Southwood 1966).

Four-wheel drive vehicles, trail cycles, and horses in addition to foot travel were used during the dry seasons. Snow machines and snowshoes were used to operate the winter traplines and to track wolverines. Each radio relocation site was recorded in detail considering habitat or cover type, ground type, ground condition, elevation, aspect, slope, topography, and proximity to road, burns, and clear cuts. Topographic maps, aerial photos, habitat type maps, and knowledge of the area enable accurate classification of aerial relocation sites. Habitat and cover types were delineated according to Pfister et al. (1977). Data on small mammal density and diversity were collected from representative habitat types, elevations, and aspects by Ramirez and Hornocker (1981).

The seasonal range and habitat preference data were separated into calendar seasons. These dates correspond to the major climatic and weather changes that affect wild species in the area.

Scats were collected in an effort to determine food habits. None was collected unless there was no doubt it was from wolverine. In addition, individuals were tracked in snow in a further attempt to determine predatory behavior and food habits.

Results

Capturing and marking

Twenty-four individuals were captured and marked during the 5-year period (Table 1): four during the winter of 1972–1973, five in 1973–1974, five in 1974–1975, seven in 1975–1976, and three in 1976–1977. That cumulative total included nine adult males, eight adult females, and seven subadults (two males, five females). The total included 11 males and 13 females. A total of 14 325 trap nights was required for the 24 captures; 11 additional wolverines were captured but escaped from the traps. A 5-year total of 60 820 km was traveled by motor vehicle, snowmobile, and cross-country skiis in tending the trap lines.

Ten individuals, three males and seven females, were recaptured a total of 74 times. In addition, five marked wolverines were caught by commercial trappers; this afforded additional information on movement and range.

In addition to "observations" gained from recaptures, observations were made on free-ranging wolverines. Two mature males, Nos. 10 and 13, were sighted by others not connected with the project. D. Biggins and S. Wirt sighted No. 13 on different occasions in spring and summer, respectively, in 1975. R. Redmond sighted No. 10 at Spotted Bear bridge in February 1976.

Wolverines were also tracked in snow throughout the study; a total of 203 km was recorded following individual wolverine tracks. Wolverine tracks, as well as other carnivore tracks, were also recorded each time they were encountered on the trap lines. The numbers of tracks recorded of each species, but not necessarily followed, are summarized in Table 2. Table 2 also provides an estimate of the relative abundance of carnivorous species inhabiting the study area.

TABLE 1. Wolverines captured in northwestern Montana during five winters, 1972–1973 through 1976–1977

Winter	Adult males	Adult females	Subadults		Total
			Males	Females	
1972–1973	1	1	1	1	4
1973–1974	1	1	1	2	5
1974–1975	2	2	—	1	5
1975–1976	3	3	—	1	7
1976–1977	2	1	—	—	3
Total	9	8	2	5	24

TABLE 2. The number of carnivore tracks encountered in wolverine study area during five winters, December 1972 through April 1977

Species	No. of tracks encountered
Wolverine	373
Coyote	3225
Weasel	1071
Marten	442
Lynx	221
Fisher	58
Cougar	26
Bobcat	15
Fox	10
Mink	1

Mortality

Eighteen mortalities were recorded during the study. Eight of these wolverines were marked. Three marked wolverines, adult female No. 6, subadult female No. 20, and adult male No. 5, died of "natural" causes. Fifteen wolverines, nine males, five females, and one of unknown sex, were known to be removed by commercial trappers during the five winters; five of these were marked. In addition, six individuals, four males and two females, were caught by trappers in the South Fork drainage the winter before our study began.

Feeding habits

Analysis of 56 scats collected in winter shows that food items taken as carrion occur more frequently than those presumably taken as live prey (Table 3). Elk and deer occurred in 27% of the scats, domestic cow and horse occurred in 27 and 18% of the scats, respectively. We believe that most of these items were taken as carrion.

Movement, range, and habitat utilization

Information from 10 individuals recaptured 74 times and from 5 animals caught by commercial trappers provided an indication of range, movement, and habitat utilization. Twenty wolverines, 9 males and 11 females, instrumented with radio transmitters provided the bulk of the data. Five individuals were instrumented a total of 12 times: Nos. 5 and 11 during three winters, Nos. 7 and 8 during two winters, and No. 20 in one winter. A total of 576 relocations was recorded on the 20 wolverines; these are summarized by sex, season, and year in Table 4. Each animal was relocated an average of once every 10 days for the entire study period and displayed a mean straight-line distance moved between successive relocations of 10 km.

The average distances traveled and the average interval between relocations for the 4 years radio telemetry was used are summarized in Table 5. Mean distances traveled were greater during spring and summer. Males throughout the study traveled noticeably greater distances than females. The maximum distance traveled in 3 days was 64 km for males and 38 km for females.

Seasonal and yearly range areas and proximity were computed from successive relocations obtained during calendar seasons. Figures 2, 3, and 4 depict typical ranges for male and female animals. Male No. 5 carried

TABLE 3. Frequency of occurrence of different food items in 56 wolverine scats collected in northwestern Montana

Scat contents	Occurrence: No. of scats in which item occurred	Occurrence: % occurrence
Marmot	6	11
Beaver	3	6
Snowshoe hare	9	17
Small rodents	3	6
Ungulate (deer or elk)	15	27
Wolverine or other mustelid	10	18
Porcupine	2	4
Birds	3	6
Domestic cow	15	27
Domestic horse	10	18

TABLE 4. Relocations of wolverines by radiotelemetry by sex, season, and year

Year	No. of relocations: Winter	Spring	Summer	Fall	Total
		Male			
1974	8	9	3	2	22
1975	18	32	16	—	66
1976	36	13	16	3	68
1977	16	2	—	—	18
Total	78	56	35	5	174
		Female			
1974	12	5	—	—	17
1975	47	53	53	27	180
1976	54	41	45	18	158
1977	18	16	11	2	47
Total	131	115	109	47	402
		All animals			
1974	20	14	3	2	39
1975	65	85	69	27	246
1976	90	54	61	21	226
1977	34	18	11	2	65
Total	209	171	144	52	576

TABLE 5. Average distance traveled and average interval between relocations of wolverines

Year	Winter		Spring		Summer		Fall		Average	
	Distance, km	Interval, days	Distance, km	Interval, days	Distance, km	Interval, days	Distance, km	Interval, days	Distance, km	Interval, days
					Male					
1974	3.7	1.7	7.4	13.8	18.8	19.0	—	—	10.0	11.5
1975	12.6	1.5	26.5	6.6	13.8	5.8	—	—	17.7	4.6
1976	8.8	5.0	11.3	15.7	9.5	5.7	14.5	6.7	11.1	8.3
1977	6.1	5.3	24.1	36.0	—	—	—	—	6.4	20.7
All	7.9	3.4	17.4	18.0	14.3	6.7	14.5	6.7	13.5	9.6
					Female					
1974	2.9	3.0	7.4	4.3	—	—	—	—	5.5	3.7
1975	7.4	5.4	8.8	8.1	9.0	4.8	10.1	4.9	8.8	5.8
1976	11.3	7.0	11.3	12.5	7.9	4.9	6.3	5.8	9.2	7.6
1977	8.2	6.5	6.3	8.2	6.6	14.4	5.6	21.1	6.8	12.5
All	7.4	5.5	8.5	8.3	7.9	8.0	7.4	10.6	7.9	8.1
					All animals					
1974	3.2	2.6	7.6	9.1	18.8	19.0	—	—	9.8	10.2
1975	9.0	4.1	14.6	7.6	10.5	5.1	9.2	5.7	10.6	5.6
1976	9.3	5.6	11.3	13.1	8.4	5.1	9.0	6.1	9.5	7.5
1977	7.1	5.9	12.2	17.5	6.6	14.4	5.6	21.0	7.9	14.7
Mean average	7.6	4.6	12.9	11.8	10.9	10.9	9.2	10.9	10.1	9.6

three functional transmitters over a 2-year period. Ranges shown for this animal typify those of other mature adult males (Fig. 2). Male No. 16 displayed a much less elongated range with extensive seasonal overlap (Fig. 3). Female No. 8 displayed a range pattern similar in size and shape to that of other females (Fig. 4). Female No. 11, monitored for a 2.5-year period, had the largest range, 963 km^2, of the animals studied (Fig. 5); this was somewhat atypical.

The average yearly range of male and female wolverines was 422 and 388 km^2, respectively. Two lactating females exhibited very similar, greatly reduced spring and summer ranges of 100 km^2 each.

Wolverines exhibited fidelity to a given area, but several individuals of both sexes made frequent long movements to other areas. The length of time spent away from the apparent home area varied from a few days to as long as 30 days. In all instances wolverines returned to the same area.

Both male and female wolverines used similar areas in elevation for all seasons with a pronounced trend from lower winter areas toward higher spring and summer areas and intermediate fall areas. The mean seasonal values are 1371 m (winter), 1676 m (spring), 1920 m (summer), and 1889 m (fall).

Areas of all exposures were used by wolverines; however, the easterly and southerly areas received the majority of consistent use. Large areas of medium or scattered mature timber accounted for 70% of all relocations. The remaining location sites were in ecotonal areas, small timber pockets, rocky, broken areas of timbered benches. Areas of dense, young timber were used least. Wolverines were rarely located in burned-over or wet meadow areas. Wet timber, dry timber, and alpine areas composed 23, 31, and 16%, respectively, of all relocation sites. Various types of topography were utilized. Slopes were used 36%, basins 22%, wide river bottoms 14%, and ridge tops 8%.

The widely distributed *Abies lasiocarpa* types accounted for the majority of relocation sites. Seral lodgepole (*Pinus contorta*) and western larch (*Larix occidentalis*) sites were frequently used. Table 6 presents a summary of habitat at relocation sites by season.

Wolverines selected *Abies* types on a year-round basis. Table 7 lists the relative occurrence of different types on the entire Flathead National Forest and on the Spotted Bear and Hungry Horse districts, where our research was conducted. This estimate, compiled by the United States Forest Service, separates only the *Abies* and spruce type; it makes up 26–27% of the types on the two districts. Some *Abies* may occur in the Mixed conifer category (Table 7), which makes up 15%. Wolverines, however, were located in *Abies* types 56% of the time, when all seasonal locations are averaged (Table

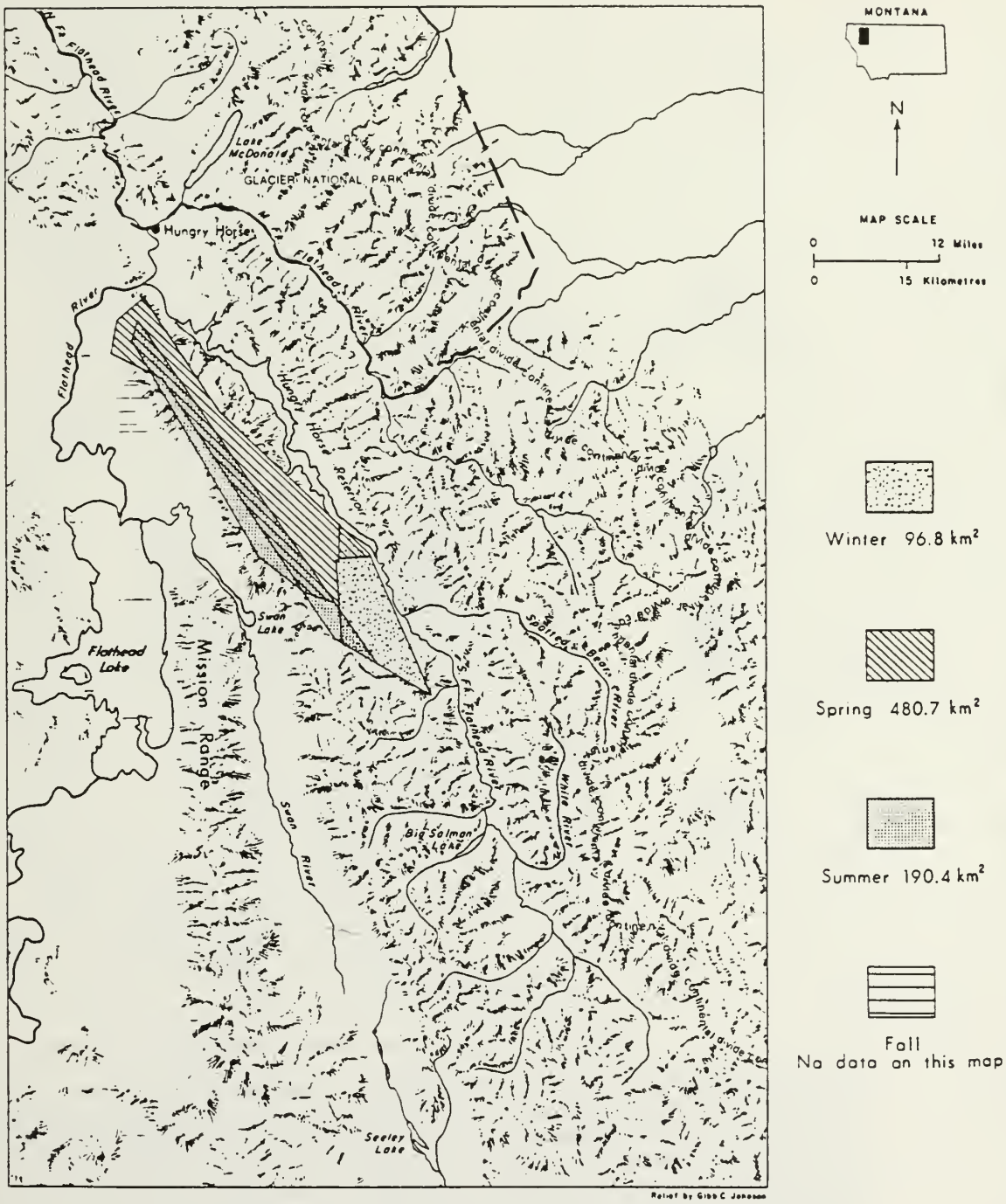

FIG. 2. Year-round range of male wolverine No. 5 in northwestern Montana.

6). There was definite strong selection for these alpine fir types in summer; these types occur at the higher cooler elevations sought by wolverines in hot weather.

No wolverines were relocated in clear cuts of any size; however, tracks were observed crossing clear-cut areas 15 times. Wolverines were located within 1 to 3 km of clear cuts and active roads 12 times. Male wolverines were found farther from active roads, clear cuts, and burns than females.

Discussion

Population estimate and characteristics

An accurate determination of population size for the entire area is difficult. Data from recaptures and from

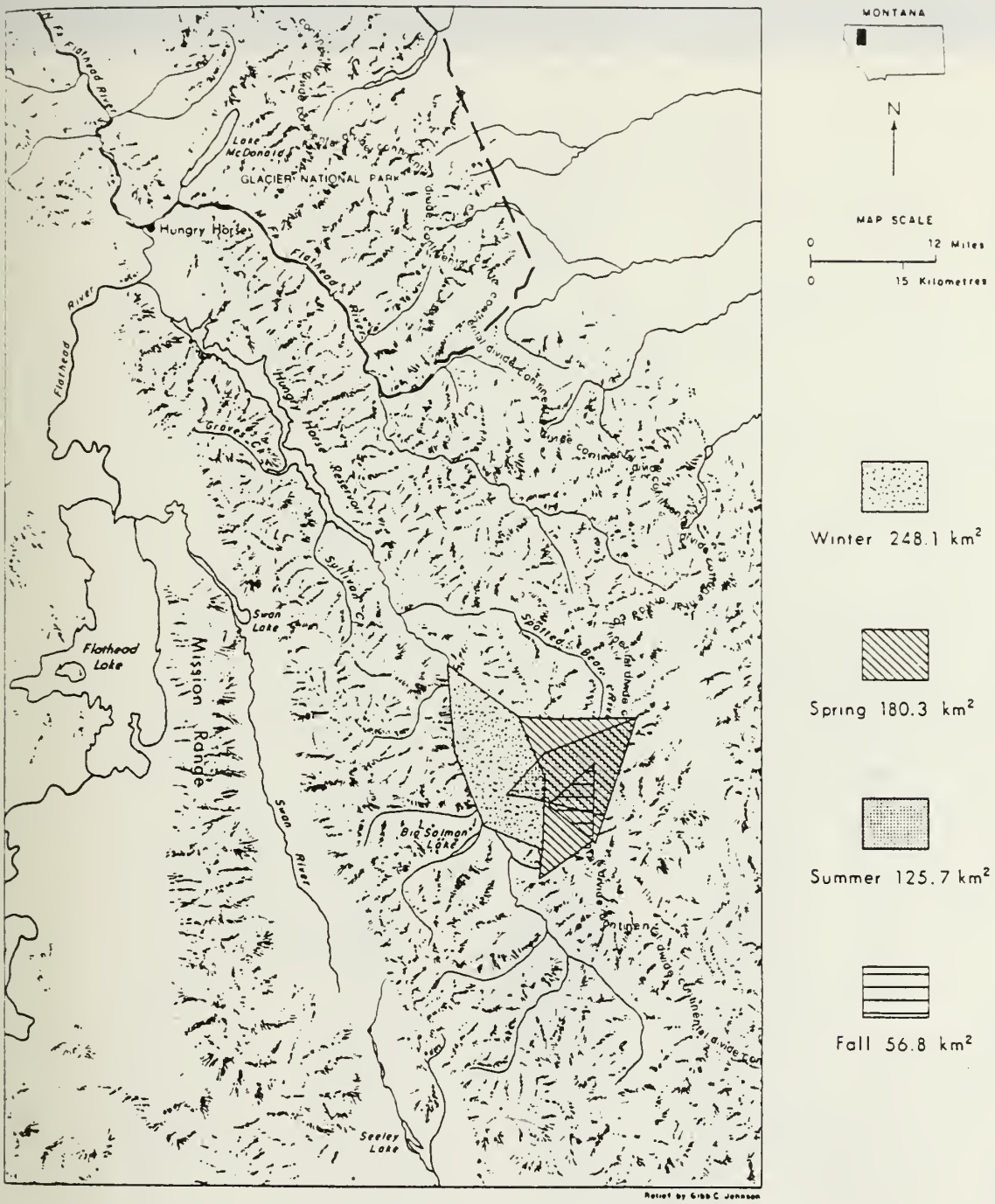

FIG. 3. Year-round range of male wolverine No. 16 in northwestern Montana.

radiotelemetry indicate that individuals constituting the population utilize a much larger area than other mustelids. Geographic barriers, such as mountain ranges and large rivers, confine some species; this is not the case with wolverines. Relative to other species in northwestern Montana, the wolverine population must be treated as regional rather than local.

We estimate a minimum of 20 wolverines on our 1300-km^2 study area based on capture–recapture data, radiotelemetry, and observations of trails in snow. Snowtracking revealed that wolverines traveled similar routes through all years of the study (Koehler et al. 1980). Koehler revisited the study area in February, 1980. On 27 February 1980 he observed fresh marking

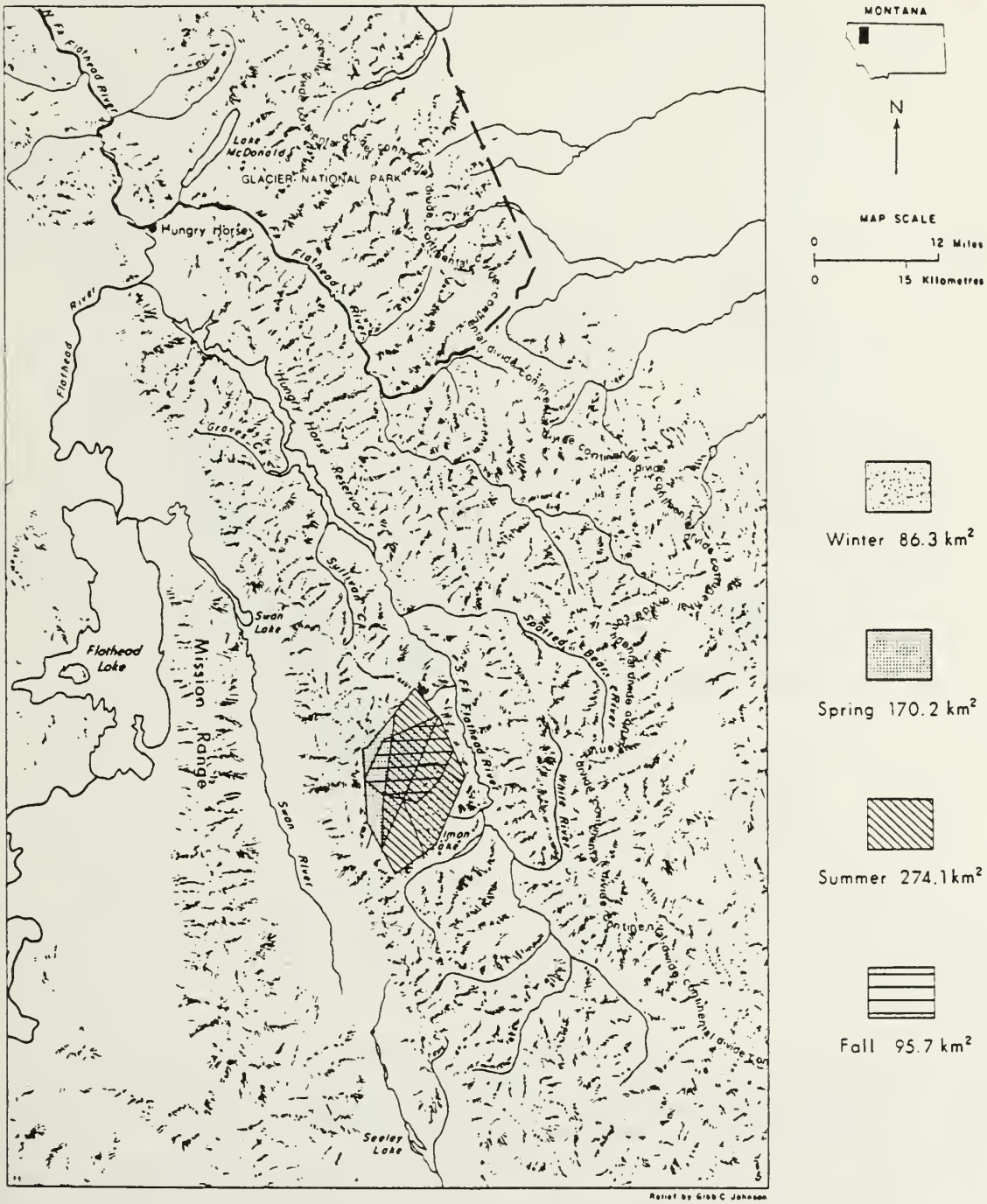

FIG. 4. Year-round range of female wolverine No. 8 in northwestern Montana.

sign on the same trees used in the winters of 1975–1976 and 1976–1977. On 29 February 1980 and 1 March 1980 he observed fresh wolverine tracks, made by different individuals, on the same trails used by wolverines during the 1975–1976 and 1976–1977 winters. Haglund (1966) and Krott (1959) made similar observations. Thus observations of wolverine tracks or trails coupled with our knowledge of the exact location of radio instrumented individuals permitted us to better estimate the number of animals present. Further, we believe that all wolverines in the South Fork drainage came to our baits at some time during the course of each winter. This

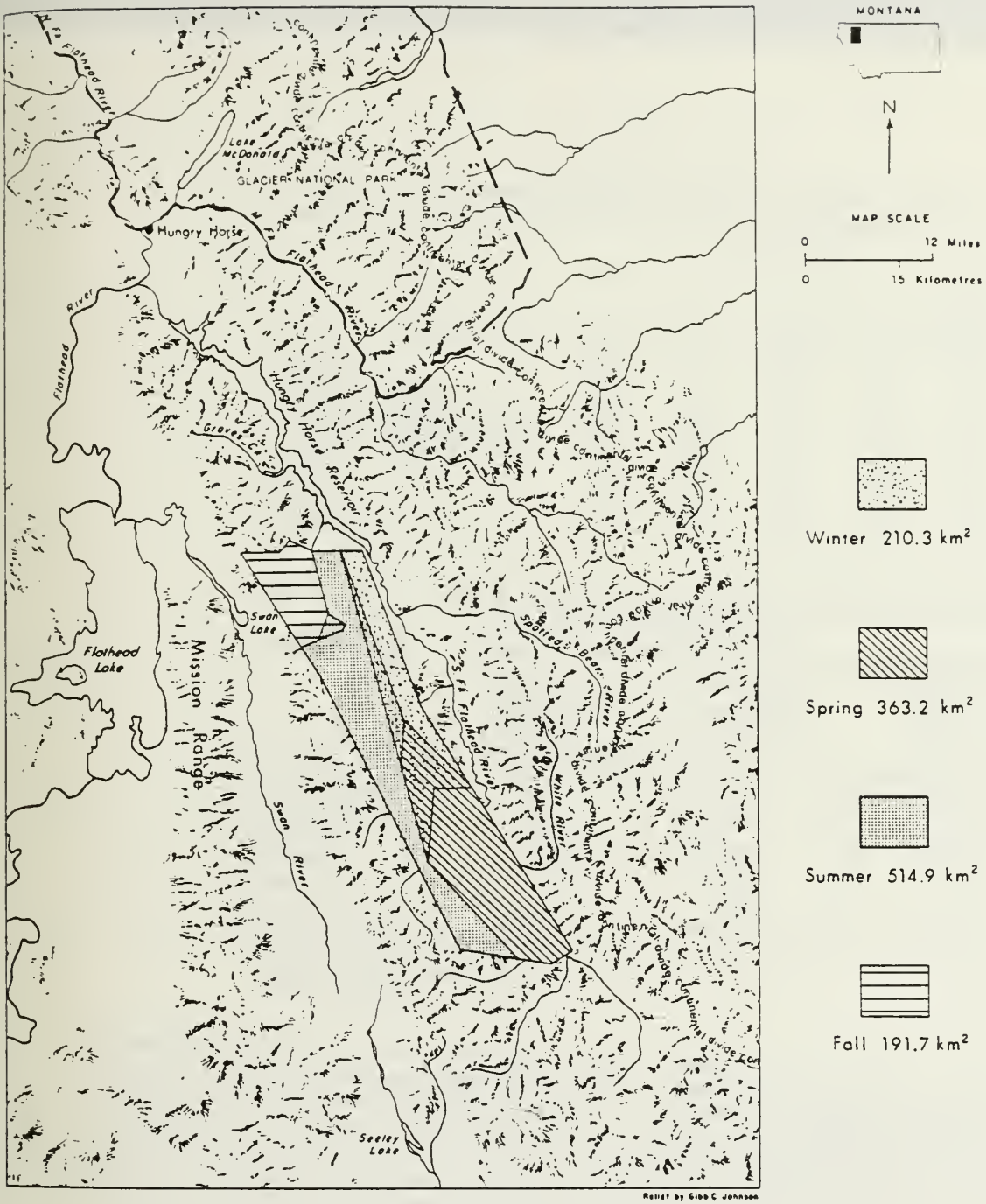

FIG. 5. Year-round range of female wolverine No. 11 in Northwestern Montana.

again is based on our knowledge of the whereabouts, the behavior, and the range and movement of radio-instrumented individuals.

We knew of 18 and 17 individuals in the winters of 1974–1975 and 1975–1976, respectively. An extremely mild winter in 1976–1977 with very light snowfall affected trapping success negatively but other known factors affecting the population remained similar. We know wolverines were present, but at higher elevations. We believe the population was relatively stable throughout the study.

Wolverines occur at low densities and even in optimal

TABLE 6. Cover types of all wolverine relocation sites by seasonal percentages

Cover type	% occurrence				
	Winter	Spring	Summer	Fall	Average, all seasons
Alpine fir	8.3	17.4	31.1	15.4	18.0
Alpine fir – spruce	27.6	17.4	36.3	23.1	26.1
Alpine fir – lodgepole pine	14.6	9.7	8.1	17.3	12.4
Douglas-fir – lodgepole pine	20.6	38.9	7.4	21.2	22.0
Douglas-fir – larch	25.5	14.6	9.2	17.3	16.7
Spruce	3.4	0.7	3.0	1.9	2.3
Shrubs	—	1.4	4.4	1.9	1.9
Herbaceous	—	—	0.7	1.9	0.6

TABLE 7. Estimate of area by major forest type for Spotted Bear and Hungry Horse Ranger districts, Flathead National Forest*

Forest type	1974 inventory % forest total Flathead National Forest	Spotted Bear† Ranger District		Hungry Horse Ranger District	
		Area, acres‡	%	Area, acres	%
Larch/Douglas-fir	28.67	76 444	30	91 378	29
Lodgepole pine	29.47	78 577	30	93 928	29
Mixed conifer	15.04	40 101	15	47 936	15
Spruce–fir	26.80	71 458	25	85 418	27
Hardwoods	0.02	53	—	63	—
Total forested	100.00	266 633	100	318 723	100

*Compiled by United States Forest Service.
†Does not include Bob Marshall Wilderness Area.
‡One acre = 0.405 ha.

habitat are less abundant than other carnivores (van Zyll de Jong 1975; Krott 1959; Quick 1953). Quick (1953) estimated a density of one wolverine per 207 km^2 in British Columbia, basing his estimate on returns from a registered trapline. Our density for a 1300-km^2 area, based on our estimate of 20 wolverines, was one per 65 km^2, or one per 25 mi^2. This greater density may be a result of a more plentiful food supply. Van Zyll de Jong (1975) stated that wolverine abundance appeared to be related to biomass and turnover of large herbivore populations, that where wolverines are still common there are large and diverse ungulate populations. Our study area supports "large and diverse" populations of ungulates: elk, (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginiaus*), moose (*Alces alces*), mountain goats (*Oreamnos americanus*), and mountain sheep (*Ovis canadensis*). This may represent a greater potential food supply, largely in the form of carrion, than that in northern British Columbia. Further evidence for a plentiful food supply is the fact that the area is inhabited by numerous species of carnivores (Table 2).

Mortality

Three of the eight marked wolverines that died during the course of the study were lost to natural causes. A pathologist at Washington State University examined No. 6, an old appearing female, and placed the cause of death as "suppurative metritis." The uterus was badly infected and contained decomposed tissue, possibly a retained fetus. Dr. T. Bell, who performed the necropsy, stated that this is not uncommon in mustelids. Wolverine No. 5, an old appearing male, and wolverine No. 20, a subadult female, starved. Both were examined by personnel of the Montana Fish and Game Department Animal Disease Laboratory.

Natural mortality in wolverine populations is extremely difficult to assess, especially in forested mountainous areas. Several species, including golden eagle (*Aquila chrysaetos*), mountain lion (*Felis concolor*), black bear (*Ursus americanus*), and grizzly bear (*Ursus arctos*), are capable of killing wolverines, particularly younger inexperienced wolverines. Burkholder (1962) stated they may occasionally be killed by wolves (*Canus lupus*) in Alaska.

One instance of a possible predation attempt on a wolverine in this study warrants mention. Female No. 11, first captured as a subadult in 1975, had had its entire muzzle torn away. We at first speculated this might have occurred in a fight with another wolverine. We discounted this when subsequent snow tracking and radio tracking of all wolverines showed no overt intraspecific strife of any kind. Captured again in 1976, this same wolverine had several deep, serious wounds on its neck and the back of its head. They appeared to be talon or claw wounds and were badly infected. We held the animal, treated it with antibiotics until it appeared recovered, and released it. We believe these wounds were inflicted by a mountain lion; at least four lions inhabited the area.

Van Zyll de Jong (1975) alludes to food availability as a factor in changes and distribution of wolverine populations. The fact that two of our marked animals starved supports this observation. It is interesting to note that both starved animals appeared to rely heavily on our baits for food just before their deaths; both visited bait stations frequently and both were recaptured a total of 24 times. It is also notable that one was very old, the other a subadult less than 1 year old.

Van Zyll de Jong (1975) further states "of the biotic factors in the wolverine's environment, predation by humans appears to be the most likely factor to have affected the number of wolverines." Clearly this was the situation in our study. Of 18 known mortalities in the five winters from 1972–1973 to 1976–1977, 15 were human caused. In addition, six were known removed by trappers the year before our study began. Wolverines are highly susceptible to trapping because they travel widely and are readily attracted to baits. Any of the adult wolverines captured in our work were missing one or more toes and many had broken teeth. We believe many of these mutilations were the result of encounters with leg-hold traps.

Reproduction

Rausch and Pearson (1972) found an average of 3.5 fetuses per pregnant female in Alaska and speculated that an average of 2.02 kits survived. Pulliainen (1968) found a mean litter size of 2.5 in 161 litters in Finland. Dr. P. Wright of the University of Montana analyzed all reproductive tracts collected from trapper-killed wolverines in northwestern Montana during our study. In 15 tracts in preimplantation condition he found a mean of 2.93 corpora lutea. In six specimens with implanted embryos or fetuses he recorded a mean of 2.17. This is significantly lower than the count of corpora (3.4) and fetuses (3.5) found by Rausch and Pearson (1972) in Alaska and the Yukon. Our sample size is too small to draw any firm conclusions, but combined with other observations, it appears productivity in our area may be lower than in Alaska.

The sex ratio in our area was roughly 1 male : 1 female; we captured 11 males and 13 females. If we accept Rausch and Pearson's (1972) survival rate or effective reproduction of 2.0 kits per litter, and assuming that at least one-half the available females bred each year, then a minimum of 10 new individuals could be added to our population annually. We know, however, from our capture–recapture data, that not all females produce young every year or every 2 years. Female No. 11, captured in 3 successive years, did not have young or appear pregnant; the same was true for others captured in subsequent years. In fact only two of the eight females mature at the time of first capture appeared pregnant. Therefore, we believe that no more than half the females present on our area were reproductively active in each of the 5 years of our study.

There is general feeling among field personnel in the Montana Department of Fish, Wildlife and Parks that wolverines are increasing in numbers. There is some evidence wolverines are repopulating historic ranges outside our study area (R. Weckwerth, personal communication). Dispersal of young from our study area is indicated by the return of marked trapper-killed wolverines in the Blackfoot River drainage to the south, the Middle Fork Flathead River to the north, and the Swan River on the west. Our data indicate a stable population on the study area proper; dispersal may be acting to maintain that stability.

Feeding habits

Wolverines are adapted for carrion feeding; Haglund (1966) stated that their skull structure, dentition, and strong jaws allow them to feed on frozen meat and to crush large bones. Various authors point out the importance of carrion in the wolverine's diet (Pulliainen 1968; Rausch and Pearson 1972; Teplov 1955 cited by Heptner and Nasimovitch; Krott 1959) and carrion appeared to be a mainstay in their winter diet in our study. Analysis of 56 scats collected in winter (Table 3) showed that elk and deer occurred in 15, or 27%, and domestic cow and horse in 15 and 10, respectively. We believe the elk and deer were taken in the form of carrion; horse meat was probably taken at our bait stations. The domestic cow was probably obtained from commercial trapper's baits or carcasses beyond the boundaries of our study area. The varied food habits depicted in Table 3 correspond to a similar pattern found by Myhre and Myrberget (1975) in Norway.

Wolverines possess an extremely keen sense of smell and can locate food under deep snow. Different individuals during the course of our study came directly to our bait stations. Backtracking revealed some came directly to the baits from distances exceeding 3.2 km (2 mi). Learning was probably a factor with some wolverines but the fact remains the baits were initially located by scent.

Our bait stations actually functioned as food "caches," referred to by Krott (1959) and others. Beyond that we found little evidence for caching. Small chunks of meat were sometimes carried away from our bait stations, and local trappers and hunters tell of sighting wolverines carrying elk or deer bones and scraps. We interpreted none of these instances as constituting caching behavior any different from other carnivores. Cached food in our study area would quickly be discovered and consumed by numerous other carnivores unless closely guarded. Further, food cached in summer or fall, not eaten by other scavengers, would decompose. It appears that caching of food, to be important in wolverine population dynamics, could be functional only in areas where other scavening species are scarce and where permafrost exists.

We snow tracked wolverines for many kilometres and it did not appear they "hunted" in the sense a skilled predator hunts. Our observations agree with Haglund (1966): "The tracker often gets the impression that the wolverine is out trying to find something to eat rather than to prey for game." We found no evidence of wolverines preying on game animals, nor did it appear they even attempted to take game species. This contrasts with the observations of Pulliainen (1965), Haglund (1966, 1974), and Makridin (1964) where wolverines preyed on reindeer and moose. Gill (1978) observed wolverine predation on a Dall sheep lamb and speculates that such predation on sheep in the area might be more common than previously believed.

Wolverines in our study did kill smaller prey, such as marmot (*Marmota caligata*), snowshoe hares (*Lepus americanus*), and different species of rodents. Snow tracking revealed that wolverines hunted brush piles, log jams, and heavy cover. P. Ramirez, on 1 March 1977, observed three occasions where a wolverine entered "tree wells," areas immediately under dense, low-growing conifers where snow does not accumulate. In two of these "wells," it killed and ate a rodent, probably a white-footed mouse (*Peromyscus maniculatus*) and a red squirrel (*Tamiasciurus hudsonicus*). Tracks and blood spotting on the snow gave evidence of kills. Tree wells, often completely bare of snow, provide easy access to the ground surface for small mammals; wolverines routinely entered these areas.

Marmots occurred in 6, or 11%, of the 56 winter scats (Table 3). To obtain marmots in winter, wolverines would have to locate them in hibernation dens. We believe this is the case; radiotelemetry indicated some wolverines spent considerable time at high elevations in winter. It appears they entered the under-snow burrows in slide rock or talus slopes and took hibernating marmots. Marmots in this area enter hibernation dens in August; we discounted caching in summer and fall for the reasons already discussed. Messick and Hornocker (1981) documented badgers (*Taxidea taxus*) feeding underground on hibernating ground squirrels in Idaho, and Teplov (1948) found that female ermine (*Mustela nivalis*) live mainly under the snow in Russia during the deep snow period, "rarely showing themselves on the surface." They fed almost exclusively on small mammals, voles and shrews under the snow.

We were unable to locate scats in summer or to gain quantitative information on summer food habits. Food is more available in spring and summer, and we believe wolverines take a wide variety of food. Krott (1959) found carrion, small mammals, insects and insect larvae, eggs, and berries in the summer diet; we believe this was the case on our study area. We were unable to attract wolverines to large freshly killed carcasses in summer, even though radiotracking revealed that wolverines came very close to these carcasses. This further supports the contention that other easily attainable food was abundant.

Ramirez and Hornocker (1981) found unusually high densities of Columbian ground squirrels (*Spermophilus columbianus*) in certain vegetative types on the study area. Radiotracking showed that wolverines spent considerable time in certain of these areas, particularly in spring. Early in spring, male ground squirrels burrow up through snow fields to the surface. They establish territories and await the later emergence of the females (Shaw 1925). There is much fighting often resulting in serious injuries. We believe wolverines preyed heavily on the squirrels. Battered male ground squirrels, engaged in territorial activity and frequent intraspecific fighting, would be quite vulnerable to such predation.

Movement and range

Wolverines in northwest Montana utilize large seasonal and yearly ranges. Males tended to make more direct, longer movements than females. Females generally used their ranges with a progressive travel pattern directed toward a more uniform coverage. Males more often traveled to the extremities of their range in relatively shorter periods than did females. Frequent seasonal and yearly range coincidence between males and females was noted, particularly during the breeding season.

We believe that food availability is the primary factor determining movements and range in our area. Breeding activity influenced seasonal movements of males but not females. Food is apparently more available, either as carrion or prey, in the mature or intermediate timber stands preferred as wolverine habitat, especially edge and ecotonal areas around cliffs, slides, blowdowns, basins, swamps, and meadows. These habitats also were preferred by fishers (*Martes pennanti*) radio tracked concurrently in this study, and by a marten (*Martes martes*) population in the Selway–Bitterroot Wilderness

Area in Idaho (Koehler and Hornocker 1977). Cover provided by mature or intermediate timber is also important in habitat selection. Wolverines appeared reluctant to cross openings of any size such as recent clear cuts or burns. Tracking revealed that wolverines meandered through timber types, hunting and investigating, but made straight-line movements across large openings. Tracks further indicated they often ran or loped across such openings. We found, in the course of snow tracking different individuals a total of 203 km, that they often bedded in snow on open outcrops. These were all in timber types which afforded cover.

Temperature also influenced summer movements. Wolverines of both sexes moved to higher cooler elevations and traveled less during daylight hours. They remained at these high elevations throughout the summer.

The scavenging lifestyle of this species dictates seasonally long movements, a relatively large home area, and a solitary existence. Our data support van Zyll de Jong's (1975) contention that the wolverine is a seasonal scavenger on the fringe of the main links of the food web. He further states "The wolverine's niche explains the relative rareness of the species in the community compared with the efficient hunters among the carnivores that act as providers, and it implies a direct relationship between the biomass and turnover of large herbivore populations and the abundance and distribution of wolverines."

The wolverine is not a serious competitor with the efficient hunter carnivores on our study area, and because of its relatively low density, probably does not compete significantly with other scavenging species. Some of these species, such as marten and coyotes, are also efficient hunters and need not rely on carrion. Wolverines are capable of displacing the smaller scavenging species in a direct confrontation. This is not the case with black bears and grizzly bears, two species with feeding habits similar to that of the wolverine. In late fall and early spring these species may compete directly with wolverines for available carrion. Large bait carcasses placed by us in summer to attract wolverines attracted grizzlies but no wolverines.

Territorial defense was found to be essentially nonexistent in Montana wolverines (Koehler et al. 1980). Home areas overlapped between individuals of the same and opposite sex. Wolverines scent marked, but as Koehler et al. (1980) point out, this serves to maintain the solitary nature of the species, maintaining spacing in time but not area. It seems that strict maintenance of a territory would be extremely difficult for a species that ranges as widely as the wolverine. Further, strict territorialism does not appear to be advantageous to a species dependent to a large extent on carrion. A system which provides for flexibility of movement to areas of carrion abundance would appear to be more successful.

It should be pointed out, however, that we were unable to establish the *characteristics* of our population. That is, we could not determine, for some individuals, if they were permanent residents, transients, or dispersing young adults. While some marked individuals were in the population for a minimum of 3 years, others were not. It may be that mortality was severe enough to keep the population in a "state of flux" by removing individuals before they could establish tenure. Mortality was obviously not excessive enough to reduce population size, but it is possible it contributed to behavioral instability within the population. If this was the situation, any inherent territorialism did not operate simply because individuals did not have sufficient time. Hornocker (1976) believes this is the situation in different populations of Idaho mountain lions. Unexploited populations showed a highly refined system of territorialism (Hornocker 1969; Seidensticker et al. 1973); individuals in populations that were exploited year after year were not territorial at all (Hornocker 1976).

We believe that, within the primary Rocky Mountain Range, wolverine populations are composed of widely ranging associative individuals. These individuals show fidelity to a particular area, or range, but sometimes move from this area for extended periods of time.

Myrberget et al. (1968) recorded similar movements in Norway. One three-footed male was tracked as far as 40–45 km outside its normal range. Movements of wolverines in Montana are not apparently affected by rivers, reservoirs, highways, valleys, or major mountain ranges.

Management implications

Wolverines are regarded as pests throughout much of their range in the world and little has been done toward their conservation. The species' habit of raiding traplines, food caches, and cabins in some areas has resulted in liberal or unlimited hunting and trapping seasons and even the payment of bounties. Its relative low value as a furbearer has further contributed to the lack of initiation of more stringent conservation measures.

Conflict between wolverines and humans in Montana is minimal but until 1975 the wolverine was classed a predator and unlimited killing was permitted. The Montana Fish and Game Commission initiated more stringent regulations in 1975. Trapping seasons were established and a limit of one wolverine per licensed trapper per season was placed in effect. The annual take has declined markedly despite the fact that some wolverines are trapped incidentally to the taking of other furbearers.

Wilderness or remote country where human activity is limited appears essential to the maintenance of viable wolverine populations. We found, however, no differences in wolverine density between the wilderness and nonwilderness portions of our study area, nor was wol-

verine movement, habitat use, and behavior different. Marked wolverines used both areas and several individuals' home areas overlapped both wilderness and nonwilderness. The nonwilderness portion, about one-half of the study area, is used by humans primarily for logging and recreation. Logging roads and foot trails provide access to river and stream bottoms and lower elevations during summer and fall months. Loggers, summer recreationists, and hunters make considerable use of these areas. The whole area, however, is bordered by rugged, relatively inaccessible mountains. Radio tracking indicated wolverines moved to these high, essentially wilderness areas in summer. Food availability in the higher elevations and cooler temperatures were factors influencing wolverine behavior. This acted to effectively separate wolverines and humans.

In winter, the whole nonwilderness portion is "snowbound" and human activity is practically nonexistent. Wolverines used the lower elevations in winter, again influenced by food availability in the form of carrion and small mammals.

Hikers and horseback recreationists use the trail system extensively in the Bob Marshall Wilderness in summer, and there are numerous hunting parties in the fall. Again the same factors acting to separate wolverines and humans in the nonwilderness operate here. In winter, the wilderness receives practically no human use.

Clear cuts have altered the nonwilderness portion substantially (see Ramirez and Hornocker 1981). These areas functioned in a similar manner to burns in the wilderness, relative to small mammal habitat. Such habitat changes can enhance herbivore and small mammal populations and thus increase the food supply for predatory species. In such habitat manipulations, however, with wolverine ecology in mind, consideration should be given to size, shape, and aspect of individual clear cuts. Wolverines in this study preferred basins, southerly and easterly slopes, and edge and ecotonal areas. These areas ideally should be left intact. Further, use of roads built in logging operations should be strictly regulated, particularly in winter. If higher inaccessible country is adjacent to clear-cut areas, wolverines will separate themselves naturally from human activity in summer. In winter and early spring, however, human access on snowmobiles or all-terrain vehicles could bring about disturbance and conflict, not to mention ease of access for fur trappers.

Regional, rather than local, populations must be considered in any management program. Our study area was large, relative to that for other species, yet it became clear we were dealing with a local unit of a regional population. Individuals routinely traveled far beyond the boundaries we arbitrarily, but because of logistics, necessarily set. By traveling widely in a short period of time, individual wolverines give a false impression of abundance. Tracks encountered in widely separated major drainages, often divided by high mountain ranges, may in fact be made by the same individual. This should be taken into account when unit or area harvest regulations are set.

Because of their scavenging nature, wolverines come readily to bait and are vulnerable to skilled trappers. In areas where enhancement of wolverine populations is the goal, bait trapping for all species should be curtailed. Further, seasons should be adjusted for closure in late winter and early spring when young are born. Females with newborn young are limited in their ranging and foraging and are especially vulnerable to easily obtained trap baits.

Wolverine populations in northwestern Montana survived the years of unlimited hunting and trapping solely because of the vast expanses of official wilderness and remote, essentially wilderness habitat. These areas functioned as both refuge and reservoir for wolverine populations. With more stringent harvest regulations now in effect, with cessation of nonselective control measures aimed at other species, and with adequate wilderness habitat, wolverine populations should be secure in Montana.

Acknowledgments

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Wolverines in Western Wyoming

Abstract

New records of the wolverine (*Gulo gulo*) from western Wyoming during the past two decades suggest a population increase for this region.

Although the wolverine is considered rare and is protected by Wyoming Game and Fish Department (1977), its status in western Wyoming remains uncertain (Weaver and Clark 1979). This note reviews historical literature and presents 50 new wolverine reports (Fig. 1) for western Wyoming, not including Yellowstone National Park.

According to Coues (1877:49), "Mr. C. Hart Merriam . . . procured a specimen on the Yellowstone River, Wyoming, in August, 1872." Thomas (1952) states that a Mr. W. H. Hill treed with dogs and shot a male wolverine in January 1899 near Kendall, Wyoming. Long (1965) listed only eight additional reports for 1900-1960, all from northwestern Wyoming. Houston (1978) recorded 27 wolverine reports in and immediately adjacent to Yellowstone National Park 1970-1978. Winter distribution of wolverines in the Park generally coincided with ungulate winter ranges where carrion was available.

We compiled recent reports from 1) field interviews with outfitters and other backcountry users during summer and fall, 1977-1979; 2) telephone interviews with and written inquiries of trappers, hunters, outfitters, and other experienced backcountry users; and 3) records of Wyoming Game and Fish Department (WGF), Grand Teton National Park (GTNP), and Bridger-Teton National Forest (BTNF). Reports were evaluated according to the reliability of the observer, conditions of the observation, and/or the quality of detail provided. Numerous reports were omitted from this note for lack of detail, but all examined fell within the geographic area delineated herein. Details of reports are available from the authors.

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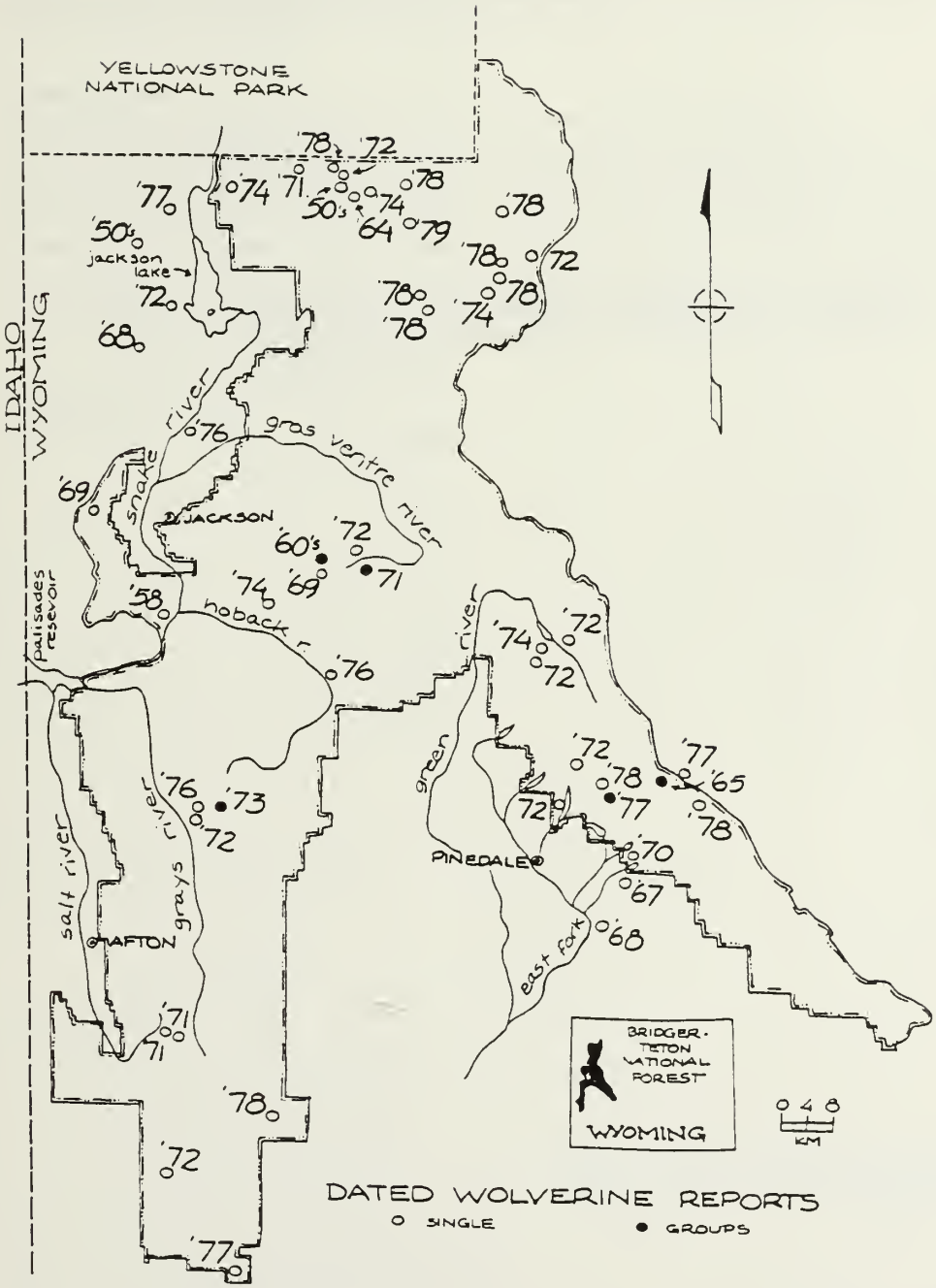

Figure 1. Location and year of 50 new wolverine reports in western Wyoming. Open circles indicate solitary animals; shaded circles, two or more wolverines (usually a family).

Wolverines occurred throughout the major mountain ranges of western Wyoming (Fig. 1), including areas farther south than previously reported. The apparent increase

of reports may reflect increased human use of remote areas, an extension of wolverine range, or both. We concur with Houston (1978) that the ban on poisons for predator control on Federal lands (Executive Order No. 11643) should benefit carrion-feeders such as the wolverine.

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been raised in captivity for the production of fur since the middle of the nineteenth century, but only in recent years has mink raising become a major industry. Wisconsin now leads all states in the number of mink farms and in sales of ranch minks, averaging more than one hundred thousand pelts annually. Ranch mink and trapped mink pelts combined have in normal years an annual sale value of more than $2,500,000 in the state.

Specimens examined from Wisconsin.—Total 103, as follows: *Ashland County:* Glidden, 1 (MM). *Barron County:* Turtle Lake, 5 (UWZ). *Buffalo County:* Wabasha Flats, 7. *Dane County:* Madison, 2 (UWZ). *Dodge County:* Beaver Dam, 13 (UWZ); Fox Lake, 2 (UWZ). *Door County:* Fish Creek, 6 (UWZ). *Douglas County:* Saint Croix River, 2 (UWZ); T 42 N, R 14 W, 1 (UWZ); T 44 N, R 13 W, 1 (UWZ). *Dunn County:* Colfax, 8 (UWZ). *Iron County:* Fisher Lake, 1 (UWZ); Mercer, 2 (UWZ). *Langlade County:* Post Lake, 3 (UWZ); T 33 N, R 12 E, 3 (UWZ); T 34 N, R 11 E, 1 (UWZ). *Marathon County:* Mosinee, 1 (UWZ). *Milwaukee County:* Milwaukee, 2 (MM); Wauwatosa, 1 (MM). *Rock County:* Milton, 1 (MM). *Sauk County:* Merrimac (5½ mi. N. W.), 1 (UWZ). *Vilas County:* Crab Lake, 2; Eagle River, 1; Mamie Lake, 1. *Walworth County:* Delavan, 10; Elkhorn, 1 (UWZ). *Waukesha County:* Duplainville, 1 (UWZ); Golden Lake, 2 (MM); Muskego Lake, 6 (MM); Pewaukee Lake, 15 (UWZ).

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Genus Gulo Pallas
Wolverines

Dental formula:

$$I\frac{3-3}{3-3},\quad C\frac{1-1}{1-1},\quad P\frac{4-4}{4-4},\quad M\frac{1-1}{2-2}=38.$$

Gulo luscus luscus (Linnaeus)
Wolverine

[Ursus] luscus Linnaeus, Systema Naturae, ed. 12, vol. 1, p. 71, 1766.

Gulo luscus Lapham, p. 43, 1852; Lapham, p. 338, 1853; Hoy, p. 256, 1882; Strong, p. 437, 1883; Hollister, p. 141, 1909; Hollister, p. 28, 1910; Cory, p. 353, 1912; Barger, p. 12, 1952.

Vernacular names.—American glutton, carcajou or karkajou, common wolverine, devil bear, glutton, Indian devil, *nag-giwy-giway* (Chippewa), skunk-bear, wolverene (secondary spelling for wolverine), and woods devil.

Identification marks.—A large, muscular member of the weasel tribe, the heaviest North American mustelid with the exception of the sea otter (*Enhydra*); general form and proportions quite bearlike; head broad, heavy, rounded; ears short, only slightly pointed, not prominent; eyes medium, forward-looking; nose broad and truncate, in effect almost that of a bulldog; tail rather short, about one-fifth total length, bushy; legs short and sturdy; feet semiplantigrade, relatively large, five-toed, provided with strong, curved, semiretractile claws; under fur not dense but soft, the long guard hairs abundant and rather coarse.

The general color is dark brown to almost black, paler (near buff) on the cheeks, face, and forehead, with two yellowish gray broad stripes extending from the upper shoulder region dorsad along the sides and meeting across the rump, thus producing a conspicuous dark color-patch in middle of back; throat and breast usually and belly occasionally with a few irregular white blotches; tail and feet dark. Details of molting have not been observed, but it probably has two molts annually, one in spring and one in fall.

Skull largest and widest of Wisconsin mustelids, heavily built, upper profile distinctly arched medially in postfrontal region, the prefrontal and maxillary regions being somewhat depressed; sagittal crest and lambdoidal ridge prominent, particularly in the adult male, the posterior extension reaching considerable distance (12 mm. in some skulls) beyond occipital condyles; audital bullae large and conspicuous,

Wolverine near Juneau, Alaska. U. S. Fish and Wildlife Service photograph by Henry Harmon.

Left hind foot of wolverine $\frac{3}{5}\times$.

Left femur or leg bone of GULO L. LUSCUS *from Bogie's Cave, Richland County, Wisconsin. Above, anterior view. Below, posterior view. About* $\frac{3}{5}\times$.

Skull of GULO L. LUSCUS, *Itasca County, Minnesota. About* $\frac{3}{5}\times$. *Lower jaw attached.*

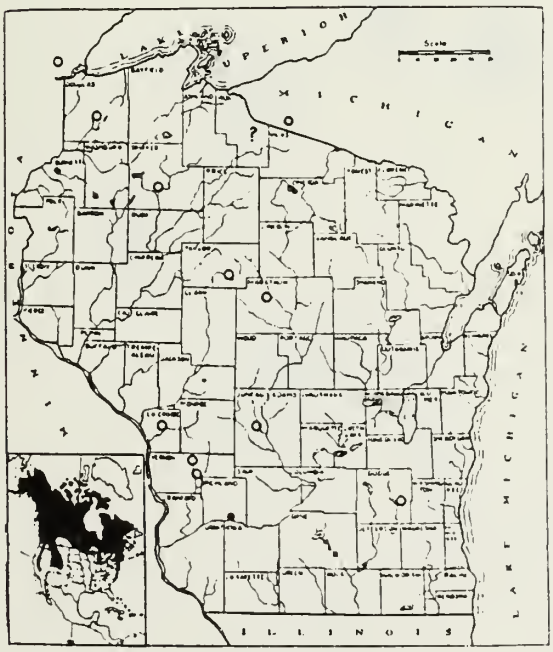
but not much inflated; nares large, placed well superiorly at angle of about 45° with horizontal axis of skull, the turbinals small, conspicuous, and many; lower jaw short and heavy, so firmly matriculated in the bony hinge to the cranium that in most specimens it cannot readily be separated. The dental formula is the same as that for the marten and fisher, but the teeth are not only considerably larger but are relatively wider and heavier and tend to be less hypsodont.

The male wolverine averages 10 per cent or more larger than the female, the skull not only being larger but also more angular with more pronounced sagittal and lambdoidal ridges. There is little age variation, although young wolverines are paler in color and display less pattern. Maturity in physical form is reached about the third year. There is some individual variation in the paleness or darkness, and in the intensity of coloration, particularly of the "saddle mark" on the back. Apparently mutations have been re-

corded as "dark brown" and "almost black" specimens, and one sure mutation as an albino individual (Jones, S. V. H., 1923: 176).

Measurements.—Total length, adult males, 960 to 1,070 mm. (37.8 to 42.1 in.); tail, 200 to 220 mm. (7.9 to 8.7 in.); hind foot, 173 to 205 mm. (6.8 to 8.1 in.). Weight, adult males, 30 to 42 pounds. Skull, adult males, length, 166 to 174 mm.; width, 99.5 to 105 mm. Total length, adult females, 725 to 947 mm. (28.5 to 37.3 in.); tail, 170 to 200 mm. (6.7 to 7.9 in.); hind foot, 170 to 180 mm. (6.7 to 7.1 in.). Weight, adult females, 22 to 28 pouns. Skull, adult females, length, 132.6 to 149.7 mm.; width, 87.2 to 96.2 mm.

Distribution in Wisconsin.—Formerly, until about the year 1870, possibly occurred sparingly over most of the state in favorable wooded habitats, but now probably does not exist anywhere in Wisconsin.



Map 66. Distribution of GULO LUSCUS. ● = *specimen examined.* ○ = *authentic records.*

Habitat.—Forests and heavily wooded areas, sometimes wandering into more open country.

Status and Habits.—Although there are several authentic records of the occurrence of the wolverine in Wisconsin, only two fragmentary specimens from the state are known. One of these is a left femur bone of an apparently adult female, and the other the distal joint end of a left femur of a young animal (both accessioned under No. 287,302, U. S. National Museum) found by the author August 21, 1920, among bones of the raccoon, bobcat, and other animals mixed with the surface soil on the floor of Bogie's Cave (sometimes called Bogus Cave), Sec. 35, T 9 N, R 1 E, about two and one-half miles west of Gotham, Richland County. The deposit was some 60 feet inside the entrance to the cave where very little daylight penetrated, and the bones appeared to be remains of animals that died there or, less likely, that had been skinned by trappers and the bodies left (Jackson, 1954: 254). Bogie's Cave is about 25 miles southeast of Kickapoo River, Vernon County, where Fred Mather and his trapper companion, Antoine Gardapee, took two wolverines in October and December, 1855 (Mather, 1896: 330, 349). Although the locality has been recorded as Bad Axe River (Schorger, 1946: 90) and was called such by Mather in his original account, he further states:

> As near as I can make out from the map of Wisconsin in a school atlas of to-day we were on the fork of the Bad Ax River in what is now Vernon county, and just north of Readstown; but there was no town, village or settlement on the river that we saw or heard of when we went up it in 1855. At any rate we were near the main forks of the river, and our cabin was between the streams (Mather, 1896: 371).

Other parts of Mather's account clearly indicate that they ascended what is now known as the Kickapoo River and came back by the same route. The site of their cabin camp probably was in or near Sec. 35, T 12 N, R 3 W, opposite the mouth of the stream now called Camp Creek. Two mounted specimens in the Milwaukee Museum that were labeled "Wisconsin" were recorded by me with the comments, "but as there are no other data we consider the record unsatisfactory" (Jackson, 1908: 14). Later, Cory says these specimens "may or may not have been actually taken in the state" (Cory, 1912: 355). They probably came from Colorado.

The Wisconsin Historical Society has a letter written July 5, 1876, by Charles Mann to A. L. Kumlien, Busseyville, Wisconsin, asking him what he would

charge to mount the skins of two wolverines from Colorado. Mann was corresponding secretary of the Natural History Society of Wisconsin, predecessor to the Museum. It therefore seems very improbable that the Museum's specimens are of Wisconsin origin (Schorger, 1946: 90).

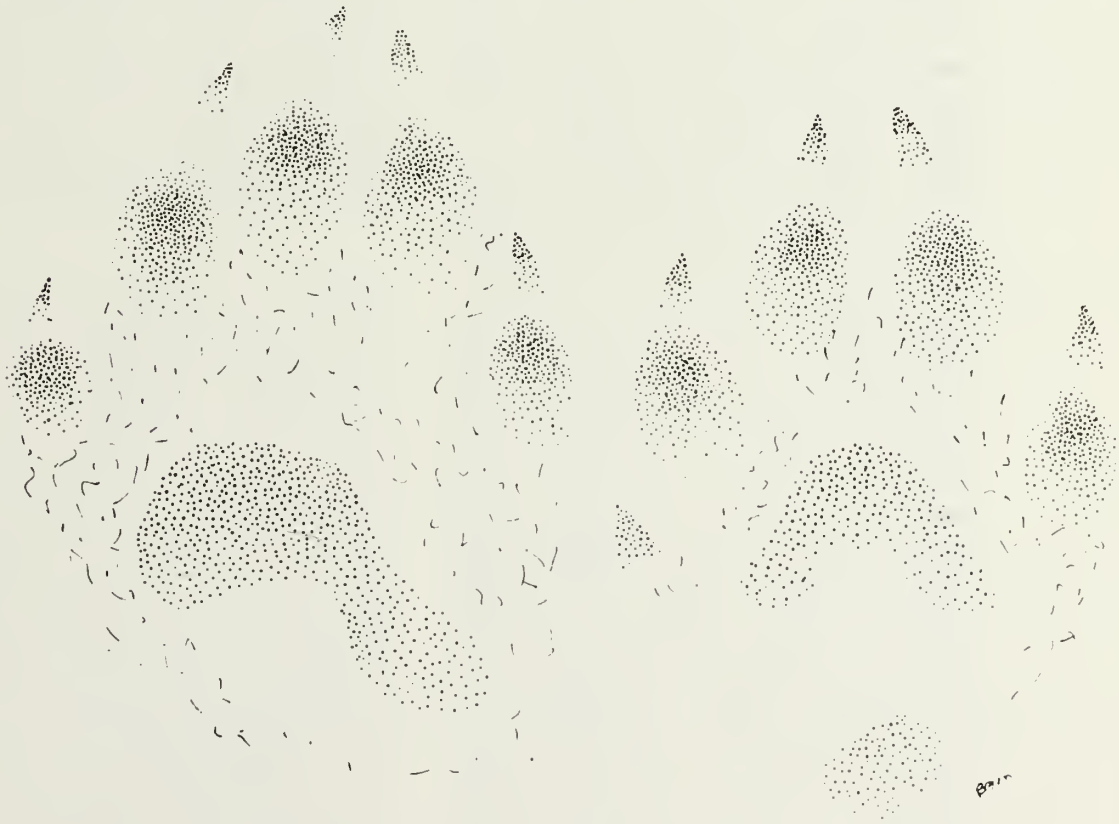
At the meeting of the Wisconsin Academy of Sciences, Arts, and Letters, July 19, 1870, the following donation to the Museum was acknowledged: "A wolverine (*Gulo luscus* Sabine) killed in Juneau County, and presented by Hon. J. T. Kingston, of Necedah." (Trans. Wis. Acad. Sci., 1: 186, 1872). The collections of the Academy were destroyed in the burning of the State Capitol, February 27, 1904. . . . The Medford (Wis.) *News*, June 8, 1876, mentions that among the animals presented for bounty in Taylor County, since January 1, was one wolverine (Schorger, 1948: 295).

Elsewhere, Schorger (1942: 29) cites a newspaper record for the spring of 1870 for Big Rib River, Marathon County. One was recorded by Hoy (1882: 256) as taken in La Crosse County that same year, and Hoy further states that they "are occasionally taken in the timber." There may be some doubt about the validity of the 1870 La Crosse County record, since many newspapers in the state mentioned the Big Rib River wolverine simply as trapped "in the pinery."

Another good record comes from Chief Warden Barney Devine and George Ruegger of Radisson in their report that a Mr. Sig Tuesulla trapped a wolverine in the vicinity of Radisson, Sawyer county, in 1922. Other records for Wisconsin are as follows: July, 1883 (Weekly Telephine [Fairfield]) "Lawn Keyes, Burnett, killed a wolverine on Horicon Marsh a few days since, weighing 31-1/2 pounds" (Scott, W. E., 1939: 26).

There are records for Gogebic County, Michigan (Burt, 1946: 144), and St. Louis County, Minnesota (Johnson, C. E., 1923: 54), both of which adjoin Wisconsin. The wolverine probably was always scarce in Wisconsin. I have found no positive records of commercial sales of its pelt,

Tracks of wolverine. Left, right hind foot. Right, right fore foot. ¾×.



though it may have been so highly prized by the natives as not to be bartered. An individual wolverine may travel great distances, and although there is no research information on its home range, it is believed to be extensive, at least 30 to 50 miles in diameter.

Nearly all of our knowledge of the habits of the wolverine is from observations outside of Wisconsin. The animal is solitary, seldom being found in the wild with another of its kind, except the mother with her kits or a mated pair. It is wary, and is seldom seen except when trapped. Its tracks are quite distinctive when clearly marked, being somewhat like those of a wolf or huge dog, but relatively wider, and usually showing the presence of the fifth toe, the heavy hairiness of the sole, and the characteristic divisions of the sole-pad of the forefoot. In heavy snow or very soft ground or muskeg the belly of the animal may drag a furrow, but otherwise the animal makes no trails or runways except at the entrance to its den. Its habit of plundering trap lines and fouling traps and trapped animals with urine, feces, and scent from its anal glands announces its presence to those familiar with the animal.

Although primarily nocturnal, the wolverine is frequently out during daylight hours. Cold weather and snow do not bother it, and it is active throughout severe winters as well as during milder seasons. It is known to wander alone many miles from its old home, and may rarely establish a new one, but it does not truly migrate. Usually it keeps its home within a few miles of the place of its birth. Its usual gait is a sort of gallop or series of jumps, much like that of a mink or weasel, but at times it walks in a lumbering movement. It is chiefly terrestrial in its activities, yet climbs fairly well, ascending trees by climbing the trunk from the base (Grinnell, G. B., 1921), or rarely by jumping from the ground to a low bough (personal letter to the author from A. H. Twitchell, Flat, Alaska, March 27, 1927). Swimming apparently is not to its liking, and though slow in the water, it progresses firmly and steadily. It also runs slowly and heavily, and although no careful studies have been made of its speed, it probably does not exceed ten miles an hour. It can be overtaken by a fast human runner.

Possibly the chief means of communication between wolverines is through urine and the anal scent glands, the scent and urine being deposited on objects, particularly near food left by the animal, possibly more of an ownership signal than real communication. Except for grunts and growls when it is irritated, the animal in the wild is rather quiet. One that I observed in the National Zoological Park, Washington, D. C., on June 2, 1928, was uttering a low-pitched, slow, not loud grunt that was not unpleasant to the human ear. The wolverine has a bad reputation as to disposition, based perhaps on a lack of real knowledge regarding its habits and behavior. It is as a rule not aggressive, but will attack and fight when molested, particularly the female with her young. Most mammals, even larger carnivores, retreat to safety when a wolverine appears, which may be due to fear of the fighting power of the wolverine or to dislike of its fetid odor. The result is the same in either case, for often the intruder profits by enjoying the food left by the vanished. It is easily treed by a barking dog, yet when cornered will outfight any dog. Trappers and explorers have told many stories about wolverines following a trap line for miles and fouling both traps and trapped animals by its glandular secretions, urine, and excrement, eating such bait and trapped animals as it fancied, and even destroying traps. Other trappers, however, have maintained that a wolverine may follow a trap line and eat squirrels or other meat used for bait, but does not molest trapped martens or destroy traps (A. J. Cardisky in Grinnell, Dixon, and Linsdale, 1937: 262). Probably the strength and sagacity of the wolverine have been greatly exaggerated, but it is without doubt physically powerful for its size and has tremendous endurance. It is no more mentally alert than others of its tribe, such as the fisher or the marten, but its inquisitiveness, persistence, endurance, and strength make it appear cunning. It is not especially difficult to trap, yet sometimes escapes from a trap because its large foot may not provide a good trap hold, and it may gnaw or pull itself free. Of its senses, those of smell and hearing are well developed, that of touch moderately so, but its sight is poor. Longevity of the wolverine is unknown, but its life expectancy in the wild is probably not more than 8 to 10 years and its potential longevity possibly near 18 years.

Reproduction of the wolverine, based on specimens procured in Alaska, has been studied by Wright and Rausch (1955: 354–55):

> Adult females taken in October, November, and January showed unimplanted blastocysts in their uteri and inactive corpora lutea in their ovaries. A late-January and an early-February specimen had implanted embryos of 22 and 68 mm. crown-rump length, respectively. Two early-April specimens were lactating but not pregnant. . . . The wolverine has a long period of gestation like many of the other mustelids. The breeding season is not precisely known, but it probably occurs in mid-summer.

The wolverine is blind at birth and has slight if any indication of hair. Its first fur is pale creamy buff, much paler than that of the adult animal. The baby develops rather rapidly, and when five or six months old parts company with its mother, brothers, and sisters, and shifts for itself. When one year old, it is nearly full grown. There is one litter a year. The mammae are eight, four abdominal and four inguinal.

The wolverine makes little provision for a nest, and is content to find shelter in a shallow cave or rock cleft, or under a rock, bank, or fallen tree, where by pawing and twisting it makes a depression 24 to 30 inches in diameter and about 6 inches deep, sometimes lining it scantily with leaves, grass, and bits of fur. The nest site is usually evident by tracks leading to it. There appears to be no special sanitation, though the occupant as a rule leaves the den to urinate or defecate.

The name "glutton" is often applied to the wolverine on account of its habits of consuming ravenously quantities of almost anything. It is primarily a meat eater, and captures most of its prey, though it is also an extensive scavenger and eats quantities of carrion. Either through choice or on account of meat shortage, it sometimes eats quantities of wild berries. In Wisconsin, the wolverine probably chiefly preyed upon such animals as snowshoe and cottontail rabbits, beavers, woodchucks, squirrels, chipmunks, and mice of various species, as well as rarely upon birds such as grouse and waterfowl. It may possibly have killed a white-tailed deer very rarely, for in other regions it has been known to attack and kill a reindeer and a small moose. Its method of attack is to pounce on the back of its prey. Its slowness of gait would not allow it to "run down" a deer, but it might pounce from a hidden position. Fawns undoubtedly were sometimes killed by the wolverine.

Man is the only important enemy of the wolverine. Not only do trappers catch the wolverine for the value of its fur, but they and other woodsmen take especial delight in killing it on account of its reputation as a robber and fouler of traps and caches, and because of its other reputed misdemeanors. Bears, pumas, and other carnivores much larger than the wolverine are reported to leave food or prey without putting up a fight on its approach. Sometimes a wolverine may be killed by quills from a porcupine it has devoured. The life and feeding habits of the wolverine are such that one might expect the animal to have many parasites, both external and internal. No information is at hand on the external parasites. Internal parasites include the fluke *Opisthorchis felineus*; the tapeworms *Bothriocephalus* sp. and *Taenia twitchelli*; and the roundworms *Dioctophyme renale* and *Soboliphyme baturini* (Erickson, 1946: 503).

The wolverine was never plentiful enough to have any pronounced economic effect on the welfare of the state. It is an interesting mammal that we wish was still a part of our fauna. Its food habits were nearly neutral, as much on the beneficial as the detrimental side. It produced a durable, luxuriant, and beautiful fur that seldom reached the fur trade, the pelt being so highly prized locally as not to enter commercial channels. The fur is said to be one of the few that will not cover with frost when breathed upon in freezing weather. I have never seen mentioned the sale of a wolverine pelt in any of the bills of lading of the early fur sales in Wisconsin.

Specimens examined from Wisconsin.—Total 2, as follows: *Richland County:* Bogie's Cave (sometimes called Bogus Cave), 2 1/2 miles west of Gotham, in Sec. 35, T 9 N, R 1 E, 2 (one left femur and one part of left femur recovered from deposit of cave floor).

Selected references.—Grinnell, G. B., 1926; Grinnell, J., J. S. Dixon, and J. M. Linsdale, 1937: 251-70; Jackson, H. H. T., 1954; Schorger, A. W., 1942: 29; 1946; Scott, W. E., 1939: 26.

of Neotropical plant communities is generally at an ecological equilibrium somehow determined by amount of precipitation—the wetter the site the greater the species diversity. The most important factor in explaining the greater species richness of Amazonia compared to other parts of the Neotropics is higher β-diversity with strong differentiation of species specialized for the different edaphic conditions that characterize Amazonia. Sites on richer soils have more species than sites on poorer soils, although soil type is distinctly subsidiary to precipitation in determining species diversity. The role of local endemism (i.e., γ-diversity) in contributing to the overall picture cannot be meaningfully evaluated until many more general collections from throughout Amazonia are available.

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Alwyn H. Gentry

Ecology of Wolverines in an Arctic Ecosystem

Grant Recipient: Philip S. Gipson, Alaska Cooperative Wildlife Research Unit, University of Alaska, Fairbanks, Alaska [1]

Grant 2110 To study the ecology of wolverines in the Arctic.[2]

Fieldwork, completed in August 1980, totaled 18 months (including all months except December and January) over a 3-year period beginning in May 1978. Figure 1 shows the location of the study area—a region about 50 by 100 km in size lying north of the Arctic Circle. During the study 23 wolverines were captured, 22 of which were instrumented with radiotelemetry collars (Table 1). All but 4 of the collared animals were relocated from the air at least once, for a total of 830 sightings. During the three field seasons wolverines were observed from the ground at dens and rendezvous sites and on hunting forays and were observed from the air hunting, scent marking, and breeding. While tracking wolverines with a snow machine, we collected scats, located snow tunnels, and recorded scent marks, caches, food items, and travel routes.

In addition to the fieldwork, wolverine carcasses were collected from trappers and hunters outside the study area. The carcasses were necropsied and data were collected on body size, age, injuries, internal organ weights, stomach contents, and reproductive condition. Skulls and, in some cases, entire skeletons were donated to the University of Alaska mammal collections.

Four areas of wolverine ecology emphasized during this research will be treated separately in articles for scientific journals and below. More detailed results are presented in Magoun's Ph.D. dissertation, 1985. Where data analysis is sufficient, preliminary results are presented in the following sections.

[1] Audrey J. Magoun, also of the Alaska Cooperative Wildlife Research Unit, was the principal investigator of this study.

[2] Additional funding agencies were: U. S. Fish and Wildlife Service, Alaska Department of Fish and Game, National Wildlife Federation, American Petroleum Institute, Wildlife Management Institute, Pope and Young Club, Interior Alaska Trappers Association, Sigma Xi, and the National Rifle Association.

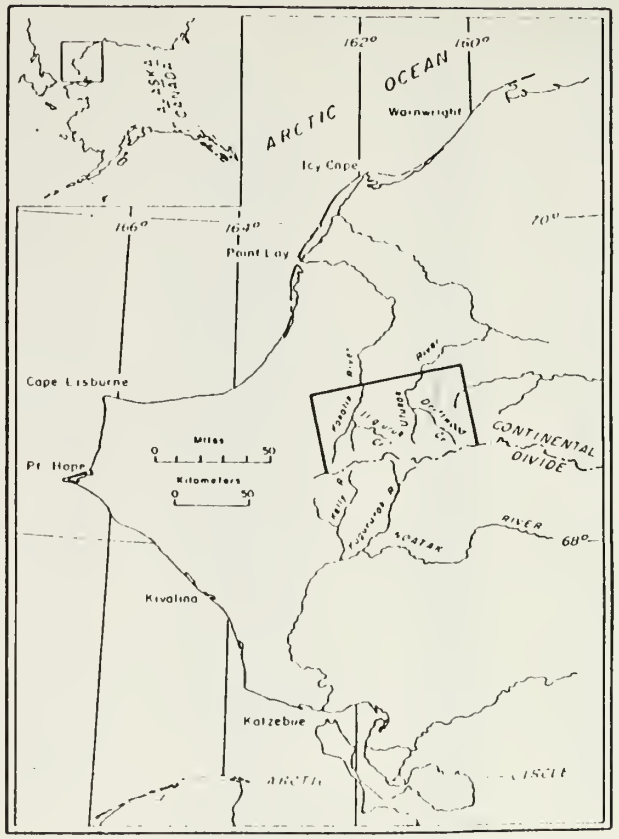

FIGURE 1. Location of the study area

HOME RANGE AND MOVEMENTS

We have adequate data to determine the home ranges of 12 individual wolverines. Figure 2 shows home ranges of those collared in 1978. We also constructed home ranges on a month-to-month basis for three female wolverines—two adults and a juvenile—to show seasonal variability in home-range size and shape (see Figure 3). Ultimately ranges will be constructed for all wolverines with six or more relocations per month so comparisons can be made between different sex and age groups. Some

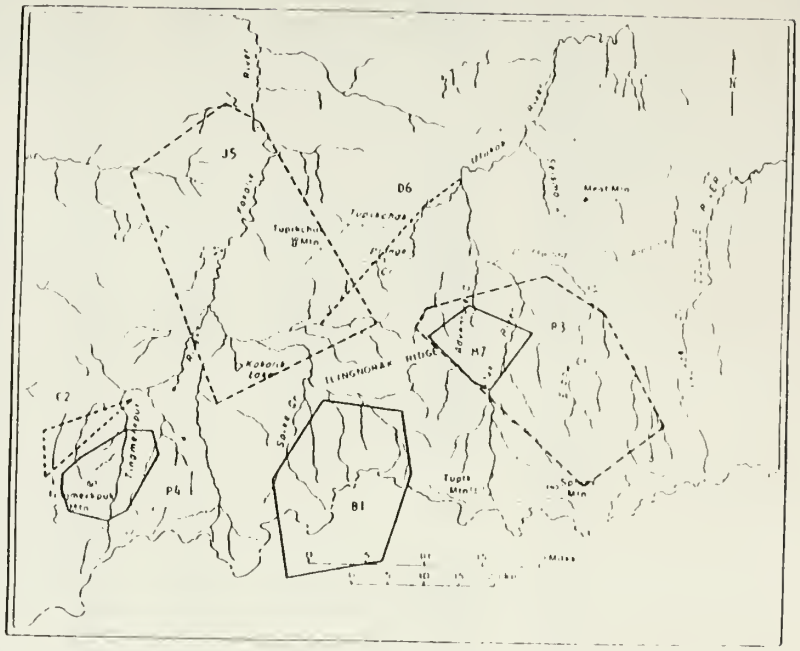

FIGURE 2. Home ranges of wolverines radio-collared in 1978. Solid lines are females; broken lines are males. Male D6 only had three locations.

factors that could influence observed differences include breeding condition, food availability, and the presence or absence of kits.

The distances between sightings also varied seasonally (see Figure 4). Relocations of wolverines were irregular due to budget restrictions and weather conditions; but when possible, they were made at least every four days during 1978 and every two days for 1979 and 1980. The two-day interval provided the greatest possible number of data points and a consistent means of comparing the movements of different individuals and of the same individual within different years. Since wolverines do not travel in straight lines, in any two-day period their actual movements cover a significantly greater distance than is indicated on our figures drawn by connecting locations of sequential sightings.

Rates of travel calculated from radiotelemetry sightings can be misleading. For this reason, a number of wolverines were observed from the air continually for one hour during which their exact movements were re

TABLE 1. Information on Wolverines Captured in the Study Area, 1978–1980

Wolverine	Sex	Age*	Date of Capture	Body Length** (cm)	Hind Foot Length (cm)	Front Foot Width (cm)	Neck Circum. (cm)	Chest Circum (cm)	Head Circum (cm)	Ear Length (cm)	Shoulder Height*** (cm)	Weight (kg)
C2	M	S	15 April 1978	84/106	18	--	--	52	--	--	--	13.1
B3	M	A	15 April 1978	84/106	20	--	--	52	--	--		15.8
J5	M	A	17 April 1978	81/103	16	--	--	46	-	--	--	12.9
D6	M	A	17 April 1978	84/106	18	--	--	--	--	-	-	12.9
D8	M	J	29 June 1978	--	17	--	27	36	--	--	41	9.1
H2	M	A	7 May 1979	85/110	19	--	35	48	--	4.0	34/47	14.5
F03	M	J	12 May 1979	51/62	15	8.0	22	33	--	4.0	30	3.6
			30 June 1979	71/89	18	8.0	28	37	-	4.0	25/36	
			19 August 1979	90/111	19	8.0	33	44	--	4.5	32/44	10.9
			19 November 1979	120/133	18	8.5	31	45	--	4.5	35/48	12.4
H4	M	J	12 May 1979	49/57	44	8.0	23	32	--	4.0	31	3.6
			27 June 1979	67/88	17	8.0	28	36	--	4.0	29/39	7.7
			4 November 1979	114/128	19	10.0	34	48	--	5.2	37/48	15.4
H7	M	A	29 June 1979	82/104	19	8.5	36	45		4.2	-	
K20	M	A	23 February 1980	93/109	18	9.5	36	46	--	4.8	36/48	13.6
B21	M	A	28 February 1980	87/96	20	10.0	37	48	38	3.5	33/49	15.4
B1	F	A	15 April 1978	72/94	16	--	--	47	--	--	--	49.5
P4	F	A	17 April 1978	79/83	15	--	--	43	--	--	--	8.6
			29 June 1979	80/99	16	7.5	32	38	--	--	30/42	9.3
M7	I	A	29 June 1978	--	--	--	--	--	--	--	--	10.9
			21 April 1979	85/104	18	--	29	40	--	5.0	-	10.4
			23 March 1980	82/100	18	9.0	30	38	38	5.0	31/42	9.5
R9	I	S	16 October 1978	78/101	17	8.0	30	42	--	--	42	10.6
H10	I	A	16 October 1978	74/94	16	--	30	39	--	--	38	9.5
			4 November 1979	78/96	18	8.5	31	42	33	4.7	28/41	9.5
			24 February 1980	76/92	18	8.5	29	42	34	4.5	29/40	10.2
B11	I	S	7 May 1979	70/93	16	--	30	37	--	--	30/40	--
D15	I	J	29 May 1979	47/57	13	7.0	24	33	--	3.0	23/31	3.8
			2 July 1979	61/81	17	7.0	27	36	-	--	27/35	7.7
			14 February 1980	79/94	17	8.5	29.5	42	33	4.5	30/41	9.5
R16	I	J	29 May 1979	48.3/58.4	13	7.0	23.5	33	-	3.0	28/22	3.6
A18	I	A	2 November 1979	84/106	17	9.0	33	41	--	4.0	31/44	10.4
A19	I	A	13 November 1979	89/108	--	8.5	29.5	45.5	-	4.8	42/32	10.0
R22	I	S	18 March 1980	75/92	18	8.0	30.5	40	33.5	4.5	27/40	8.8
B23	I	S	25 March 1980	83/104	18	8.5	32	41	32.5	4.0	31/42.5	9.5

* Age: adult (A), subadult (S), immature animals over one year old, and juvenile (J), animals under one year old

** Body length: first, length from nose to base of tail; second, from nose to tip of vertebrae.

*** Shoulder height: first, height from shoulder blade to wrist; second, from shoulder blade to tip of toes.

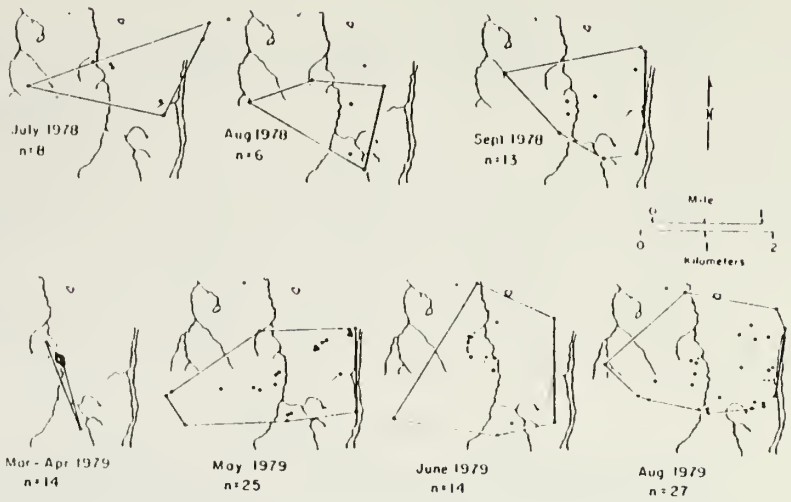

FIGURE 3. Home range by month for female M7 for 1978 and 1979. Only those months with six or more sightings are shown.

corded on aerial photographs (Figure 5). From this information, actual travel rates were computed and compared with rates of travel derived from straight lines connecting beginning and ending points. None of the one-hour periods included resting time, which would have significantly affected any calculations of travel rates.

Food Habits and Habitat Use

Analysis of scats collected during the fieldwork is under way and Table 2 presents some preliminary data. The stomach contents of carcasses collected in areas surrounding the study area will be analyzed as well. Additional data on food habits are available from observations of wolverines during radio-tracking flights or while observing wolverines on the ground. Table 3 is a summary of habitat utilization by activity for 483 radio relocations in 1979 and 1980. The study area will be mapped by habitat and the locations of wolverines in each correlated with the availability of each habitat in the wolverine's home range. The final report will discuss the seasonal availability of food for wolverines and the importance of each habitat type.

In the wolverine habitat in the Arctic, snowdrifts form along stream banks and drainage lines beginning in September or October and lasting

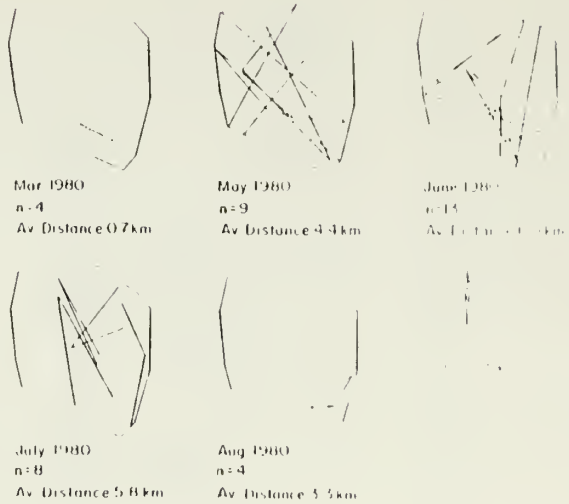

FIGURE 4. Distances between radio relocations made on alternate days for female M7. The average distance between locations changes monthly. Three consecutive radio relocations in March were in the same place, a den site.

through most of the summer. Besides providing protection from weather and predators, tunnels in the drifts provide convenient food storage sites. The tunnels are repeatedly visited, not only by the animal that excavated them but by other wolverines as well. Sketches and measurements of snow tunnels excavated during the study are being prepared.

FIGURE 5. Exact routes traveled by wolverines under constant watch from an aircraft for a period of one hour. The distance of the travel route and the straight line distance between the beginning and ending points are given.

Table 2 Major Food Items in 61 Wolverine Scats Collected, 1978-1980

Food Item	No. of Scats with Item	% of Total Scats	No. of Scats with > 50% of Item	% of Scats with > 50% of Item
Large mammal (caribou, moose)	47	77	34	72
Ground squirrel	14	23	7	50
Microtines	24	39	14	58
Bird	20	33	0	--
Vegetable	46	75	0	--

Social Behavior

From the spacing patterns we documented, adult female wolverines appear to use home ranges that generally exclude other adult females at least from April through September. The data are not adequate, however, to discuss whether or not male wolverines exclude other males from their home areas. However, it appears that males tolerate the presence of one or more females in their home areas, so that overlap occurs in the home ranges of males and females.

Data for juvenile animals are limited. Available information indicates that at least some female offspring remain in their mother's home range for more than a year. Circumstantial evidence suggests that aggressive behavior on the part of resident adult wolverines is related to the dispersal of immature animals that have remained in their mother's home range until the onset of the breeding season. Two cases of immature males dispersing from the study area have been documented; and circumstantial evidence supports the dispersal of two additional immature males and two immature females between 9 and 14 months of age.

Three agonistic interactions were observed between wolverines. Two encounters were between a radio-collared adult female and an untagged wolverine of unknown sex and age which the radio-collared female appeared to drive away. In the third encounter, a young radio-collared female (probably a subadult) was observed fighting with an unmarked wolverine, believed to be a female since it was similar in size to the collared female. (All immature animals are essentially adult size by their first winter.) The young female had only recently been radio col-

Table 3. Number of Sightings for Each Activity per Habitat Type, 1979 and 1980

Habitat	Drainages (other than river valleys)		Riparian Willow		Tussock		Sedge		Dry Hillside		Rock		Snowdrift		All Activities		
Sex	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	Total
Traveling	2	3	15	14	18	60	4	8	5	13	3	5	17	20	64(60%)	123(33%)	187(39%)
Resting	0	4	11	17	5	41	0	2	3	5	0	15	9	92	28(26%)	176(47%)	204(42%)
Hunting	0	2	2	10	8	40	1	15	1	4	1	1	2	5	15(14%)	77(20%)	92(19%)
TOTAL	2	9	28	41	31	141	5	25	9	22	4	21	28	117	107	376	483
% Occurrence per Habitat	2	2	26	11	29	38	5	7	8	6	4	6	26	31			

lared so that home-range data were not yet available for her; within two days after her confrontation, she disappeared from the study area.

Two adult males captured in April had fresh wounds on their faces. Though fighting by males was never observed, all collared adult males carried scars.

Some form of territoriality probably exists in the social system of wolverines. For most mammalian species that maintain territories, scent marking is believed to be important to territory maintenance. Scent marking—in the form of urination, defecation, or scent-gland secretion—by wolverines of all sex and age groups was observed, even by kits less than four months old. Frequent observations of wolverine scent marking were made; but it was difficult to differentiate between the types of marking unless the animal rubbed vigorously while depositing scent.

The rubbing of scent glands on terrain features was easily observed from the air; but it is also possible that scent was deposited when no rubbing was evident. Only observations of captive animals depositing scent, urine, and feces will clarify any difference in posture that occurs between marking types. Scent marking was observed while animals were traveling, hunting, and breeding. The intensity of marking varied between individuals and under different situations by the same individual.

Wolverine breeding behavior was observed in three instances, the first such observations in the wild. In 1978 a young female wolverine (R9) was observed copulating on August 6. She apparently did not produce kits from this mating, believed to have been her first. This same wolverine was observed mating with a young adult male (K20) the following year on June 11. The third observation was of an adult female (M7) and an older adult male (B21) on June 5, 1980.

Kits are born in the study area about mid-March. In 1978, a male kit (D8) was born to female M7. The following year she produced two more male kits (P13, T14) and the female in the adjacent territory produced two female kits (D15, R16). Data on the growth rate of these kits are provided in Table 1. The natal den of M7 was not located in 1978 though her capture site is believed to have been very close to the den. In 1979 this female's den was observed in April and May until she moved her kits to a new area. The neighboring female also moved her kits from her natal den about the same time. The moves were probably triggered by spring meltwater entering the dens. Human disturbance was not believed to be a factor.

Through the months of May and June, the females would periodically move their kits to new rendezvous sites, most often remnant snowdrifts with tunnels formed by meltwater. The kits would remain at the site while the female hunted. She would return to the site with food or would lead the kits to a new site where she had previously cached food

items. The kits began regularly traveling with their mother by July. By August they were spending a considerable amount of time on their own.

Play was a normal part of the social behavior of females and their kits, and continued late into the fall when kits would meet their mother in her home range. Such behavior occurred when a female (H10) and her 17-month-old daughter (D15) met at the boundary of their adjoining areas when the immature animal no longer shared much of her mother's home range. Play behavior was also observed between a juvenile male (D8) and an uncollared wolverine believed to live in an adjacent area. The male was approximately six months old and near the boundary of his mother's home range at the time of the incident. A wolverine similar in coloration to the uncollared animal was caught and collared the following year in that area and proved to be an adult female (A19).

On a number of occasions, a collared wolverine was seen in the company of an unmarked wolverine not its offspring (of that year at least). The age and sex of the unmarked animals were not known. Unless breeding behavior was imminent, these meetings were usually of short duration. On a number of occasions during May, an adult male (J12) visited an adult female (H10) with two kits (D15, R16), but the female would chase the male whenever he approached. In an observation made from the air on May 7, an adult male (J12) approached a young female (B11) (probably a yearling) while he was traveling through her home range. The two approached each other cautiously, sniffed, and separated traveling in opposite directions. This male frequently visited the female's home range in May and June. From tracks in the snow, it was evident that they spent some time together.

Population Dynamics

Population-dynamics data of wolverines in an arctic ecosystem have been gathered. Comparisons will be made with other wolverine populations and management implications will be discussed in other publications.

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internal cingulum. There are two distinct cusps posterior to the main cusp, the rear one being small. P_3 is long and narrow with a poorly defined posterior internal cingulum as in P_4. It bears a well-defined cusp posterior to the main cusp.

The P_2 which is present bears no secondary cusps. Except for its narrow width, it resembles an ordinary P_2 of a Recent coyote; however, this tooth is rotated 180° in the jaw. Although its twin is missing, the alveoli show that it was not rotated and was approximately the same size as the rotated tooth. It is easily seen from the alveoli that while the larger socket for P_2 is normally posterior to the smaller, anterior socket, this condition is reversed in the rotated tooth (Fig. 1).

There is some crowding of the toothrow caused by the extra tooth. The twinned teeth are placed partly side by side, the rotated tooth being slightly displaced medially by the (presumedly) normal P_2. Between P_1 and the anterior alveolus of the normal P_2, there is only a small space as opposed to the condition found in most coyotes. A slightly larger space is present between the rotated P_2 and P_3, while there is almost no diastema between P_3 and P_4.

TABLE 1.—*Measurements in millimeters*

Length from posterior border of alveolus of canine to anterior border of alveolus of M_1	54.5
Length from anterior border of alveolus of P_1 to posterior border of alveolus of P_4	48.0
Depth of jaw below P_4	14.5
Depth of jaw at posterior border of P_4	19.0
P_4, anteroposterior length	13.8
P_4, greatest width	5.5
P_3, anteroposterior length	12.0
P_3, greatest width	4.1
P_2 (rotated), anteroposterior length	10.0
P_2 (rotated), greatest width	3.5

Discussion.—Wood and Wood (1933) list the following 4 explanations for the presence of extra teeth: (1) mechanical splitting of a tooth germ; (2) retention of a deciduous tooth; (3) mutation producing a new tooth; (4) reversion to an ancestral condition. The specimen concerned here seems to be an example of mechanical splitting of a tooth germ. Retention of a deciduous tooth is ruled out by the size of the rotated P_2 and by the size of the alveoli of the missing P_2. Mutation producing a new tooth is also unlikely because the rotated P_2 is, in all other respects, a normal second premolar. The alveoli of the missing P_2 are similar to those of the rotated tooth and, in turn, to those of P_2 in Recent coyotes. There is no question of the multiplication being a reversion to an ancestral condition since that number was 4, not 5, premolars.

Although twinning or duplication is more common in simple peg-like teeth, it is not unknown in the more complex cheek teeth of carnivores (Guilday, 1962). Guilday reports that it is, in fact, the normal condition of M^2 and M_2 in *Otocyon*. Rotation of a twinned tooth, as in the specimen of *Canis* cf. *C. latrans*, is apparently a far less common condition, about which very little is known.

For a listing of associated fauna, see Gazin (1936).

ACKNOWLEDGMENTS

I am deeply indebted to C. W. Hibbard, Museum of Paleontology, University of Michigan, for his help in this study. I should also like to thank W. H. Burt and Emmet T. Hooper, Museum of Zoology, University of Michigan, for allowing me to study the museum's collection of Recent skeletons. The recovery of this specimen was made possible by the National Science Foundation (Project G-19458).—MARY D. FINE, *Museum of Paleontology, University of Michigan. Received 19 April 1963.*

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SECOND RECORD OF AN ALBINO PINE VOLE

A series of pine voles, *Pitymys pinetorum pinetorum*, at the North Carolina State Museum, contains an albino specimen (Number 170). Both the skin and skull are preserved. The vole, a young adult male, was taken by Mr. Jake Barnes on 4 March 1941, at Wendell, Wake County, North Carolina. Its measurements are as follows: total length 109, tail 19, hind foot 14.

The specimen appears to be a complete albino, with all parts of the body being white. Eye color was not designated on the specimen label. In all respects other than color, the vole appears to be typical of the species.

Schantz (J. Mamm., 41: 129, 1960) recorded the first albino *Pitymys* from southern Georgia. Because the skull was lacking, Schantz made no specific determination. Based on the locality collected, her record appears to be a *P. pinetorum* (Hall and Kelson, The mammals of North America, 1959). The North Carolina specimen appears to be the first verified report of albinism in the species *P. pinetorum*.—JOHN R. PAUL, *Department of Zoology, North Carolina State College, Raleigh. Received 7 April 1963.*

RANGE EXTENSION OF THE WOLVERINE IN MONTANA

Information from trappers, fur buyers and naturalists suggests that the wolverine (*Gulo gulo*) was near extinction in most areas of Montana by 1920. From that time until about 1940, the wolverine was almost unknown from Montana. Beginning about 1940, wolverines were seen and shot or trapped with increasing frequency in the northwestern part of the state. Twenty-one capture records and 20 authenticated sight records reflecting the regrowth of the wolverine population in northwest Montana through 1953 were reported by Newby and Wright (J. Mamm., 36: 248–253, 1955). At that time the majority of records of wolverine occurrence were restricted to the extensive mountain ranges along the Continental Divide.

Reports of trappers, hunters, U. S. Forest Service and Montana Fish and Game Department employees accumulated since 1953 show a continuing increase in the region demonstrated as occupied in 1953. These reports also document an extension of range to areas where wolverines had not been reported for many years. Records of 17 captures supporting this range extension can be seen in Fig. 1 and Table 1. It is significant that a 1954 canvass of Montana Fish and Game Department employees did not produce even a single report of a sighting of wolverine in southwestern Montana while a similar 1961 canvass of Department and U. S. Forest Service employees produced a number of authentic capture records of wolverine in addition to sight records not used in this report. The authors believe that this is conclusive evidence of continuing repopulation of much of the remaining wolverine habitat in Montana.

Many of the capture reports in Table 1 involve males as did many of the outlying reports recorded in the 1955 paper. This suggests that the initial invasion of new habitat is made by the wide-ranging male. Many of the additional sight and capture records accumulated from northwestern Montana since 1953 concern females with young or in-

Newby and McDougal

TABLE 1.—*Capture records of wolverine in Montana*

No.	Date	Locality	County	Sex	Collector	Examined
1	Nov. 1961	Ural Mountains	Lincoln	Unknown	Melvin Mlender, Whitefish	Report only
2	Spring 1959	Basin Creek	Jefferson	Male	Dale Clason, Billings	Report only
3 and 4	Winter 1960–1961	Basin Creek	Lincoln	Unknown	Art Baron, Yaak	Photograph
5	1957	Laurin Canyon	Madison	Unknown	Lawrence Schultz	Report only
6	Oct. 1960	Foster Creek	Granite	Male	Earl Johns, Anaconda	Photograph
7	Jan. 1961	Dry Wolf Creek	Judith Basin	Male	Reuel Janson	Carcass
8	May 1960	Flathead Pass	Gallatin	Male	Yeaden Bros., Manhattan	Carcass
9	March 1958	Basin Creek	Jefferson	Male	Joe Walsh, Butte	Mount
10	Feb. 1958	Dearborn River	Lewis and Clark	Male	Fay Overman, Augusta	Mount
11	Feb. 1957	Stickney Creek	Lewis and Clark	Male	William Perry, Cascade	Pelt and skull
12	Oct. 1954	Jackson Creek	Lincoln	Unknown	Martin Peterson, Worland	Report only
13	Fall 1955	Johnson Creek	Missoula	Unknown	Arne Karkaren, Address Unk	Report only
14	June 1959	Swamp Creek	Beaverhead	Unknown	John McDougal, Bob Jackson, Jackson	Front foot left in trap
15	July 1959	Swamp Creek	Beaverhead	Unknown	R. P. Jackson, Jackson	Captured alive
16	Winter 1961	Bannack	Beaverhead	Unknown	Vern McMannis	Skin
17	Oct. 1962	Flint Creek	Granite	Female	Stuart Markle	Carcass

mature animals, indicating the establishment of breeding populations. One of the current reports from the Big Hole Valley also is of a young wolverine.

The distribution and chronology of the records of the last 20 years suggest that reestablishment of the wolverine in Montana occurred primarily through natural dispersal from Canada and later, Glacier National Park, followed by successful reproduction. The wolverine is totally unprotected in Montana and is subject to predator control efforts on settled areas. There have been no efforts at artificial restocking. It is of interest that the fisher (*Martes pennanti*), although exterminated in much the same fashion, has not made any comparable recovery. There are no recent authentic reports of fisher occurrence prior to artificial restocking begun in 1958. Since the release of 40 fishers in 1958 and 1959, 5 of the original animals and one offspring have been reported or recovered. This number of reports from such a limited population suggests that the complete absence of such reports of either fisher or wolverine for extensive periods strongly indicated extinction of these species.—FLETCHER E. NEWBY AND JOHN J. MCDOUGAL, *Montana Fish and Game Department, Helena, and U. S. Forest Service, Jackson. Received 3 May 1963.*

WEIGHT OF A LARGE FISHER

During a live-trapping and transplanting program of fisher (*Martes pennanti* Erxleben) conducted by the Maine Department of Inland Fisheries and Game, a male fisher weighing 20 pounds and 2 ounces was caught. This animal was trapped by Forrest Smart 12 February 1962 in Sebec, Piscataquis County, Maine and was weighed on Chatillon spring-type

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DISTRIBUTION AND STATUS OF THE WOLVERINE IN MONTANA

By Fletcher E. Newby and Philip L. Wright

Wolverines (*Gulo gulo*) were probably distributed throughout the mountainous areas of Montana until the western fur trade became active. If Coues (1893) was correct in his interpretation of remarks in the journals of the Lewis and Clark expedition, possibly the earliest recorded observations of the wolverine in Montana were made in 1805 near the present city of Great Falls and in the Big Hole Valley near the Idaho-Montana border. Even as late as 1927 the wolverine population of Yellowstone Park was estimated at six or eight by Skinner (1927), but from information available from trappers and fur buyers it seems likely that in most areas of Montana the wolverine was near extinction before that time. In recent years, however, wolverines have been seen and shot or trapped with increasing frequency in the northwestern portion of the state. In an effort to evaluate this apparent regrowth of population the authors investigated many reports provided by trappers, hunters and other woodsmen. All reports which were not supported by specimens were carefully evaluated and it is believed that all presented here are completely authentic.

Although the 21 capture records date back to 1932, 18 were taken since 1939. Eleven have been shot or trapped since 1950. To our knowledge, recent sight records of wolverines began only in 1944 and since then at least twenty observations have been made. The records obtained can be seen in Figure 1 and Tables 1 and 2.

Material from eight of the wolverines taken is in the Montana State University Zoological Collection. This includes: one mounted specimen, one skin, two skulls, one skeleton complete except for the maxillae and mandibles, two skulls with skins, and one leg and foot.

It is of interest to determine whether these Montana specimens should be classed with the Southern Wolverine (*Gulo gulo luteus*) or with the Northern Wolverine (*G. g. luscus*). Since Grinnell, Dixon and Linsdale (1937) indicated that *G. g. luteus* is recognizable only by possessing smaller dentition, measure-

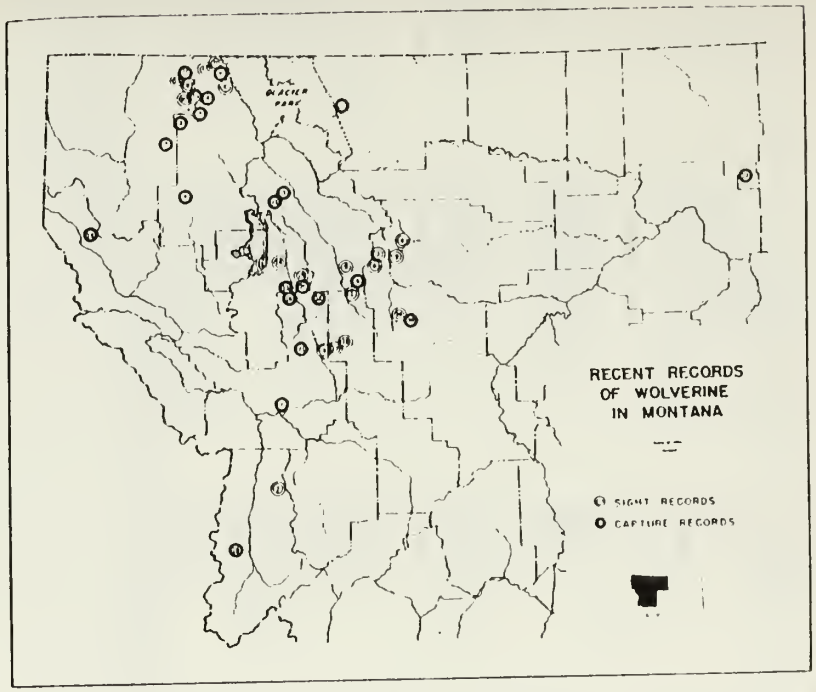

Fig. 1.—Recent records of wolverine in Montana.

ments were taken from the four skulls and compared with those presented by Grinnell, Dixon and Linsdale (1937) and also with measurements taken from a series of skulls from northern Alaska available to the junior author through the courtesy of Dr. Robert Rausch, Arctic Health Research Center, Anchorage, Alaska. Three of the Montana skulls are known to have come from males and the other is probably a male. Since Grinnell, Dixon, and Linsdale (1937) consider the tooth measurements to be critical, these data are summarized in Table 3.

The measurements of the Montana skulls in all cases but one lie within the range of the Alaskan series. Accordingly the former are regarded as belonging to the subspecies *G. g. luscus*. Parenthetically it should be pointed out that the measurements presented by Grinnell, Dixon and Linsdale (1937) of the dentition of a California male wolverine with supposed "noticeably and uniformly lighter dentition" also lie within the range of the series of Alaskan specimens. In view of this, surely the status of the subspecies *G. g. luteus* should be reinvestigated.

Lack of adequate earlier records of wolverine distribution makes accurate appraisal of the significance of recent records difficult. It is recognized that there may be a tendency for older records of observations and captures to escape notice; even so, the evidence strongly suggests an increase in population.

Although scattered individuals may have survived the intensive trapping of

TABLE 1.—*Sight records of wolverine in Montana*

No.	Date	Locality	County	Observer	Remarks
1	Mar. 1, 1944	White River Flats	Powell	Lloyd McDowell, M.F.G.D.* Horace Godfrey, U.S.F.S.**	
2	Mar. 1, 1945	Black Bear Landing Field	Flathead	Lloyd McDowell, M.F.G.D. Horace Godfrey, U.S.F.S.	
3	Aug. 27, 1947	Red Shale Creek	Lewis & Clark	Faye Couey, M.F.G.D.	2, seen by 15 people
4	1947	Teton River	Teton	U.S.F.S. Crew	
5	Aug., 1947	Headquarters Creek	Teton	Ray Gibler, U.S.F.S.	2
6	1948 or '49	Red Meadow Creek	Flathead	Ross Wilson, M.F.G.D. Lawrence Deist, M.F.G.D.	
7	Spring, 1948	Burnt Fork	Ravalli	Orville Lewis, M.S.U.***	
8	Summer, 1948	Rock Creek	Lewis & Clark	Paul Hazel, U.S.F.S.	
9	Oct., 1949	Rice Creek Ridge	Missoula	Joseph Townsend, M.F.G.D.	
10	Aug. 1, 1950	Stillwater River	Lincoln	R. T. Cloninger, U.S.F.S. J. L. Aemesegger, U.S.F.S.	4, young
11	Aug. 29, 1950	Williams Creek	Lincoln	J. L. Aemesegger, U.S.F.S.	
12	Sept. 13 or 14, 1950	Young's Creek	Powell	Wesley Woodgerd, M.F.G.D.	
13	Sept., 1951	Krinklehorn Lake	Lincoln	W. R. Ellis, U.S.F.S.	
14	June 21, 1952	Woodward Meadows	Lake	O. J. Nollar, M.F.G.D.	
15	Summer, 1952	Trail Creek	Flathead	G. M. Daugharty, U.S.F.S.	
16	August, 1952	Wood Creek	Lewis & Clark	Dan Neal, U.S.F.S.	2
17	October 18, 1952	Pyramid Pass	Powell	William McCurdy, M.S.U.	
18	May, 1953	Lion Creek	Lake	G. M. Daugharty, U.S.F.S.	
19	July 3, 1953	No. Fk. Fitzsimmons Creek	Lincoln	Wm. Maloit, M.F.G.D.	
20	Nov. 6, 1953	No. Fk. Flathead R.	Flathead	Dan Block, M.F.G.D.	

In addition, a considerable number of sight and track records have been obtained in Glacier National Park in the last fifteen years.
* Montana Fish and Game Department.
** United States Forest Service.
*** Montana State University.

TABLE 2.—*Capture records of wolverine in Montana*

No.	Date	Locality	County	Sex	Collector	Examined
1	1932	Marshall Creek	Missoula	Unknown	Robert Anderson, Polson	Report only
2	Jan., 1933 or 1934	Forks of Sunday & Advent Creeks	Flathead	Male	Tom White, Stryker	Report only
3	Winter, 1939	Pioneer Ridge	Flathead	Female	Ray Miller, Kalispell	Report only
4	Dec., 1940	Red Meadow Lake	Flathead	Female	Tom White, Stryker	Skull, *MZ**
5	Winter, about 1940	Wolk Creek-Fortine Creek Divide	Lincoln	Two—unknown	Oscar Grey, Fortine	Report only
6	Winter, about 1941	Haskill Pass	Flathead	Male	Hugh Galloway, Kila	Skin
7	Fall, 1945	Near Fish Lake	Flathead	Male	Ray Miller, Kalispell	Whole mount, *MZ*
8	Fall, about 1946	White River	Flathead	Female	H. C. Jorgenson, Polson	Skin
9	March, 1946	Teepee Creek	Flathead	Male	Louis Haverlandt, Eureka	Skin
10	Winter, 1948	Ford Creek	Lewis & Clark	Unknown	J. Hinkel, Augusta	Report only
11	Winter, 1950	Graves Creek	Lincoln	Female	W. R. Ellis, Fortine	Skin, *MZ*
12	Fall, 1951	Albino Basin	Missoula	Unknown	Big game hunter	Report only
13	Dec. 11 or 12, 1951	Teepee Ridge	Lake	Male	Glenn Clothier, Swan Lake	Report only
14	Feb. 15, 1952	Swamp Creek	Sanders	Male	Will Fox, Trout Creek	Skull, *MZ*
15	Feb. 26, 1952	Wolf Creek	Flathead	Female	Carrol Eslick, Bigfork	Whole mount
16	March, 1952	Jim Creek	Missoula	Male	John Hulett, Swan Lake	Whole mount
17	Aug. 21, 1952	So. Fk. Milk R.	Glacier	Male	Alfred Vance, Browning	Skin and Skull, *MZ*
18	Summer, 1952	Lake Como	Ravalli	Unknown	Cause of death unknown	Leg & foot, *MZ*
19	Mar. 18, 1953	Bear Paw Mts.	Hill	Male	Earl Seyler, Havre	Skin and Skull *MZ*
20	Apr. 10, 1953	Swan Valley	Lake	Female	Wm. Woodward, Missoula	Skeleton, *MZ*
21	July, 1953	Lake Elsina Area	Missoula	Two—male & female	Robert Boyce, Missoula	Report only

* Specimens now in the Montana State University Museum of Zoology.

TABLE 3.—*Tooth measurements (in millimeters) of wolverines*

		Ant.-Post. Up. canine	Ant.-Post. Up. carnas.	Trans. dia. Up. carnas.	Trans. dia. Up. molar	Max. tooth row
Northern Alaska						
Means of 18 Males from northern Alaska		11.1	21.2	12.3	14.0	53.7
Minimum		10.4	20.2	11.6	13.4	50.7
Maximum		12.2	21.9	13.3	15.0	56.3
Montana						
Red Meadow Lake	MSUZ 459	11.1	20.7	11.8	13.1	51.7
Swamp Creek	MSUZ 3845	11.0	20.5	—	14.0	56.7
South Fork Milk River	MSUZ 3901	10.8	20.4	12.0	14.0	54.0
Bear Paw Range	MSUZ 3928	11.4	20.5	11.9	13.5	51.8
California						
Yosemite National Park	MVZ 22121	10.8	20.3	11.9	13.7	51.5

early days, the distribution and chronology of the recent records do not indicate a regrowth of population due to local reproduction. It appears instead that dispersal from Canada, and later, Glacier National Park may have been responsible. Reference to Figure 1 shows that the majority of the recent records are restricted to the extensive mountain ranges along the Continental Divide in northwestern Montana. It is emphasized that there are a number of other areas of wilderness in Montana that should provide suitable habitat for wolverines. Wolverines were trapped from the Park area before establishment of Glacier National Park in 1910, but in 1918 Bailey quoted a local resident as believing them to be completely absent from the Park. Examination of National Park Service records indicated that tracks were first seen again in 1933. Since then tracks and observations have been reported from the Park almost every year. It is probable that the protected area of the Park served as a reservoir of breeding stock. Without such an area, re-establishment of the species would have been difficult, for the wolverine is completely unprotected in Montana. The establishment of closed or limited seasons on marten in later years aided in the survival of dispersing individuals by restricting the operations of trappers in wolverine habitat. Low prices for marten and Canada lynx pelts in recent years have caused an additional decline in the activities of trappers in remote areas.

Although a wolverine was taken by a trapper west of Glacier National Park in 1933 or 1934, regular reports outside the Park did not begin until 1939. In 1942, estimates of Fish and Game Department personnel placed the number of wolverines in the Whitefish Range west of the Park at four. The number of sight and kill records in that area since then indicates an increasing population. Then, after many years of apparent absence, wolverines were seen east of the Continental Divide in the Sun and Teton River drainages in 1947. Isolated reports from the Bitterroot Range in 1948 and 1952 and from the Cabinet Range in 1952 may also represent dispersing individuals.

Most remarkable of all the records is the adult male wolverine killed in the Bear Paw Mountains south of Havre, Montana in 1953. These mountains are

a small, isolated range approximately 150 air miles east of the main range of the Rocky Mountains. It seems unlikely that this small area could have concealed a wolverine population unnoticed for long, since it is an Indian reservation and is subjected to considerable trapping pressure. A report of similar nature was obtained from the trapper who took the Cabinet Mountains specimen in 1952. He reported that in the 1920's he caught a wolverine in the Sweetgrass Hills, another small, isolated mountain range about one hundred air miles east of Glacier National Park. Although this report could not be verified, the circumstances certainly parallel those of the Bear Paw record. We can only theorize that these animals reached these isolated ranges by following the broken topography and scattered timber along rivers such as the Teton, Marias and Milk which flow eastward from the main range of the Rockies. Other records that provide further evidence of the travelling ability of the wolverine have come from Washington and Idaho. Scheffer (1941) reported an adult male taken in the Okanagan Valley near Riverside, Washington, and a Boise, Idaho newspaper of March 30, 1951, carried an account of a wolverine killed by Idaho Game Department personnel near Caldwell. Both records were considered unusual for their location by local authorities and were far from areas of boreal forest.

Evidence of successful reproduction was provided by the observation of four young wolverine on the Stillwater River in 1950. Additional evidence of breeding activity may lie in four observations involving two animals each in July and August, since the breeding season in this species apparently lies in midsummer (Wright and Rausch, MS). The wolverine is reputed by naturalists to be a solitary animal and no such records of pairs were obtained at any other time of year.

It seems reasonable to conclude from the data presented that the wolverine is not at present threatened with extinction but instead may be increasing its numbers and repopulating its range in Montana. However, extensive logging operations have made rapid inroads into many areas of excellent wolverine habitat in recent attempts to control depredations of the spruce bark beetle (*Dendroctonus engelmanni*). If this situation continues our protected wilderness areas and National Parks will be the only areas remaining with suitable habitat for animals such as the wolverine, Canada lynx, marten and grizzly bear.

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WOLVERINE

The pelt of the wolverine is strong and durable. The fur wears well (Harding 1915, Kaplan 1974) and is widely used in the Arctic and Subarctic for ruffs or trim on parkas, especially on hoods; this is because rime ice or frost from a person's breath can easily be brushed from parka trim that is made of wolverine fur (Quick 1952). For this reason, many pelts do not enter the market and hence the actual harvest may be higher than that reported.

Historically the wolverine has been harvested in much lower numbers than other furbearers. Prior to the 20th century, only the sea otter was harvested (occasionally) in lower numbers than the wolverine. The low harvest of wolverines may reflect their low natural density compared with other carnivores (Hash 1987), but the wolverine is not an economically important furbearer internationally and has not been widely sought for fashion garments by the fur industry.

Prior to the 20th century, four companies contributed to the harvest of wolverines: the Hudson's Bay Company, the North West Company, American companies, and Russian companies (Fig. 12). The total North American average annual harvest ranged from about 250 pelts in the 1720s to slightly more than 2,700 in the 1790s. Generally, it increased from the low of 256 in the 1720s to about 900 in the 1760s, dropped to about 800 in the 1770s, then increased to about 2,700 in the 1790s and about 2,400 in the early 1800s. It dropped to about 700 for the 1820s, increased to more than 1,400 in the 1840s, then remained greater than 1,100 in the 1850s and 1860s. Harvests then increased to about 2,400 in the 1880s and remained greater than 2,000 in the 1890s.

Harvests of wolverines by the Hudson's Bay Company rose from an average harvest of 250 pelts per year in the 1720s to about 800 per year in the 1740s, 1750s, and 1760s. It then declined to about 200 per year in the 1780s and remained at this level until the 1820s, when it rose to about 500 per year. The harvest of wolverines then continued to rise to about 1,800 per year in the 1880s, which was the maximum average annual harvest recorded by the Hudson's Bay Company.

Where records are available (i.e., 1780s to early 1800s), the North West Company harvests of wolverines were higher than those reported for the other three companies. A maximum annual harvest of more than 1,600 pelts was reported for the 1790s.

Harvests by American companies start at about 100 pelts per year in the 1760s and increase to 900 per year by the early 1800s, which is the maximum harvest recorded by American companies. Values then decline to less than 50 per year in the 1840s. No records were obtained for the 1850s and 1860s, but starting with an annual average harvest of slightly more than 100 pelts in the 1870s, harvests rose to more than 700 per year in the 1890s.

Figures for harvests of wolverines by Russian companies are only available from the 1790s to the 1840s. The harvest by Russian companies was minor. Except for a harvest of more than 170 pelts taken in the early 1800s, the number of pelts taken annually was less than 100.

In the 20th century the North American harvest of wolverines is lower than that of most furbearers, the exceptions being the mountain lion, brown bear, and polar bear. From an average annual harvest of more than 1,100 pelts in the 1920s the harvest declined to 700 in the 1940s (Fig. 12) and remained at less than 900 until the 1970s (> 1,600) and 1980s (> 1,400).

The decline in the numbers of wolverines trapped from the 1920s to the 1960s is considered the result of a general wolverine population decline and extirpation in some areas which began during the late 1800s and early 1900s as a result of overtrapping and habitat degradation (Hash 1987). Wolverine populations also declined in Canada from the 1920s to the 1970s (Van Zyll de Jong 1975).

Canadian harvests of wolverines in the 20th century follow a similar pattern to those of the North American harvests. High harvests of about 1,000 pelts per year in the 1920s declined to less than 500 per year in the 1960s; the average harvest rose slightly to more than 700 per year in the 1970s and 1980s. American harvests of wolverines remained less than 400 per year until the 1970s, when average yearly harvests of more than 700 were obtained, and the 1980s, when more than 600 pelts were harvested annually.

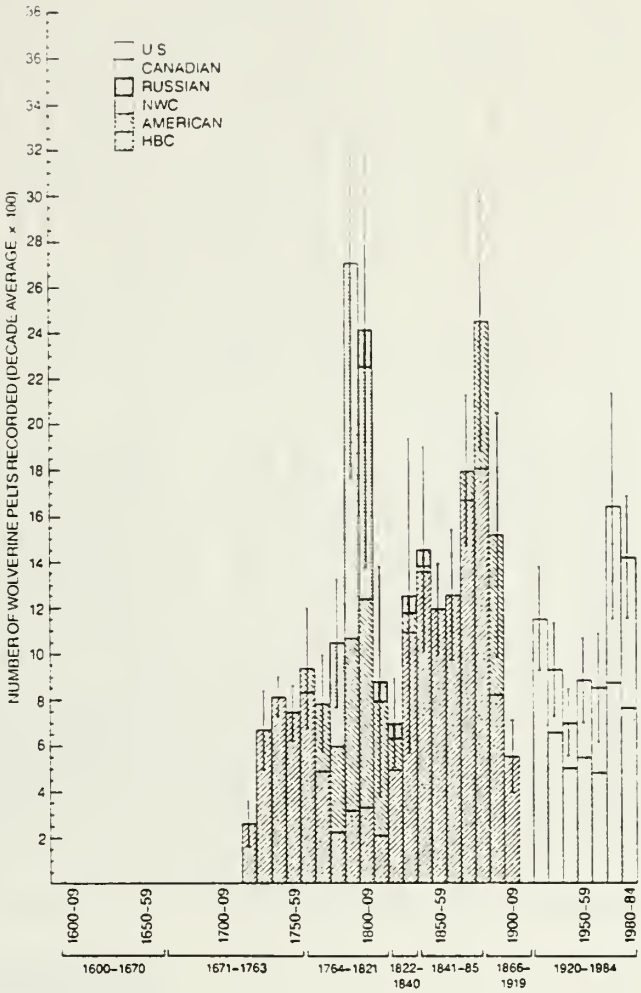

Fig. 12. Average annual harvests of wolverine pelts (by decade) in North America from the 1700s to the present.

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NOTES ON THE WOLVERINE IN ALASKA AND THE YUKON TERRITORY[1]

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Abstract: New data concerning the life history of the wolverine (*Gulo gulo*) were obtained from 1159 specimens taken in Alaska and the Yukon Territory during 1960–68. Fifty percent of female wolverines 16 to 28 months old were pregnant; 91 percent of those 29 months and older were pregnant. Wolverines apparently breed in May, June, and July. The blastocysts implant primarily in January and February, and most of the young are born in February and March. Implantation occurs from December through March and parturition occurs from January through April. Fifty four litters (*in utero*) averaged 3.5 fetuses. Most male wolverines are sexually mature when 14 to 15 months old. In males, testis weights indicate that the peak of the breeding condition is in May and June. Mean body weights of whole wolverines were: adult males, 31.2 pounds; juvenile males, 29.4 pounds; adult females, 20.7 pounds; and juvenile females, 20.1 pounds. The wolverine is not an endangered species and its habitat is reasonably secure.

The wolverine has been the object of considerable mythology throughout its circumpolar range. Much of the folklore stems from the wolverine's tendency to utilize a wide variety of food—food often gathered by another species. These habits brought the wolverine into conflict with man. As the wolverine is also equipped with powerful jaws, offensive musk glands, and an insatiable appetite common to weasels, man concerned himself more with eliminating this competitor and in furthering the folklore than with attempting to learn facts about its life history.

As the wolverine was gradually extirpated or greatly reduced in numbers, particularly in Fennoscandia and in the contiguous United States, man finally took notice and, within the past 15 years, a number of studies, in Fennoscandia and Russia, have been reported. Notable among these are the studies by Kroll (1959), Makridin (1964), Mylne (1968), and Pulliainen (1968). Meanwhile, scientists in North America have contributed little. Wright and Rausch (1955) discussed breeding biology and suggested age determination techniques, and Wright (1963) elaborated upon the earlier work. Newby and Wright (1955) and Newby and McDougal (1964) reported on wolverine population increases in Montana as evidenced by distributional records. Kurtén and Rausch (1959) reported on the taxonomic status of Fennoscandian and Alaskan wolverines, and Rausch (1959) reported on the parasites of Alaskan wolverines and noted some foods of trapped animals.

The aforementioned studies have provided a generalized picture of wolverine life history. The information shows that male wolverines are not in breeding condition during late fall and early winter. Spermatogenesis commences in late winter and is active by early spring. Winter skeletons indicate two major age-classes, adult and immature. Yearling males may be sexually mature. Wolverines breed during the summer, and unimplanted blastocysts are known from October until January. The blastocyst implants in January after an indeterminate delay, possibly as long as 7 months. Female wolverines den in a variety of habitats, generally on the surface of the ground under snow. Kits are reportedly

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Fig. 1. Study areas: Alaska and the Yukon Territory. Sample size: Alaska, 861; the Yukon Territory, 198.

born in January, February, March, and April, though the various authorities are not in agreement. Litters in dens average 2.5 kits and kits leave the dens in April and May.

Agricultural interests in Fennoscandia and Russia consider the wolverine an effective predator of domestic reindeer.

METHODS AND MATERIALS

This report summarizes the results of studies started in Alaska in 1960 by R. A. Rausch and A. W. Erickson (Erickson 1962) and those conducted in the Yukon Territory by A. M. Pearson. The material consists of 861 wolverine carcasses obtained in Alaska from 1960 through 1968 and 198 collected in the Yukon Territory from 1961 through 1968.

The distribution of the material from Alaska is shown in Fig. 1. Wolverines range throughout the mainland of Alaska and are present on some of the larger islands in the southeastern part of the state (Manville and Young 1965). The carcass collection is biased toward those areas where hunting and trapping are more intensive as revealed by statistics obtained from bounty records (Tables 1 and 2).

The carcasses from Alaska were obtained from trappers and hunters, some were obtained free, but most were obtained for a payment of $5.00 plus freight charges. Often the carcasses were exposed to a variety of treatments that tended to reduce their usefulness for study. For example, some animals died in traps before the trappers arrived and were quick-frozen at 0 F to −60 F; others remained alive and were killed by the trapper, taken to his cabin, skinned at his leisure, and then frozen.

Table 1. Summary of recorded harvests of wolverine in Alaska through 1968, as determined from pelt shipments and bounty records.[a]

Year or Period	Number	Year	Number	Year	Number	Year	Number
1798–1821	51[b]	1921	191	1937	369	1953[c]	360
1822–1842	74[b]	1922	296	1938	248	1954	300
1843–1862	1[b]	1923	296	1939	228	1955	350
1863–1876	16[b]	1924	220	1940	326	1956	200[d]
1877–1909	–	1925	360	1941	232	1957	200[d]
1910	110	1926	468	1942	164	1958	350
1911	179	1927	809	1943	92	1959	213[d]
1912	189	1928	831	1944	87	1960	420
1913	242	1929	873	1945	108	1961	444
1914	136	1930	495	1946	157	1962	383
1915	119	1931	406	1947	527	1963	415
1916	297	1932	234	1948	188	1964	551
1917	435	1933	281	1949	490	1965	402[e]
1918	816	1934	279	1950	500	1966	659
1919	546	1935	260	1951	350	1967	694
1920	561	1936	290	1952	400	1968	578

[a] Adapted from Courtright (1968).
[b] Annual mean.
[c] Bounty records start here.
[d] These may be export totals rather than country totals, in which case the totals shown are low.
[e] Bounty records not complete.

Table 2. Harvest statistics and carcasses collected 1959–68 (Alaska).

Season	Animals Bounties	Carcasses	Percentage of Total Harvest	Class of Hunter[a] 1	2	3	4	Method of Take[b] 1	2	3	4	5	6
1960	402	–	–	41			12	3	4				36
1961	444	–	–	416	10	4	6	4	407	5			20
1962	383	145	38	444	14	15	2	25	57	57			3
1963	415	113	25	246	31	27	10	37	188	52			10
1964	551	113	20	320	91	33	30	74	305	64	0	1[c]	33
1965	402[d]	112	27	235	69	88	10	33	283	33	0	6	47
1966	659	105[e]	16	463	82	105	9	65	492	46	0	0	56
1967	694	119[e]	17	509	35	139	14	78	537	44	4	4	32
1968	578	154	27	396	48	122	12	99	438	35	0	0	24
	3,730	861	23										

[a] Professional, 1; incidental, 2; recreational, 3, and unknown, 4.
[b] Ground shooting, 1; trapping, 2; snaring, 3; digging out, 4; aerial shooting, 5, and unknown, 6.
[c] Illegal.
[d] Bounty records not completed.
[e] Attempted to collect only female carcasses; some carcasses of males were donated.

The distribution of specimens from the Yukon Territory is shown in Fig. 1. Most of the carcasses were collected from a predator control program carried out by the Game Department, Yukon Territorial Government. A few were purchased from trappers, and the animals taken in summer were incidental to a study of the grizzly bears (*Ursus arctos*) in southwestern Yukon.

Predator control stations were not checked with any regularity, and animals killed there thus were often exposed to changes in environmental temperatures for 1 or 2 months. In that time, a carcass could partially thaw and refreeze several times.

The tissues of animals collected in winter from Alaska and the Yukon Territory often were subject to autolysis, which reduced the usefulness of the material and usually forced us to work with gross or macroscopic observations rather than with histological procedures.

Breeding Biology

The usable material included reproductive tracts from 366 female wolverines from Alaska and 51 female wolverines from the Yukon Territory. The ovaries and uteri were removed from partially thawed carcasses and refrozen for later examination. Measurements taken of the tracts included the length and greatest diameter of each uterine horn, the diameter of the cervix, and two diameters of each ovary. If ovulation had not taken place, or if the animal was not postpartum, the uterine horns were flushed in an effort to detect blastocysts (Hamilton and Cook 1955). Blastocysts, if found, were preserved in 10 percent formalin. The uterine horns were slit, and placental scars if present, were recorded. The ovaries were fixed for a period of at least 10 days in 10 percent formalin or A.F.A. The ovaries were sliced with a razor blade at 0.5 to 1.0-mm intervals, ovarian structures, including corpora lutea of pregnancy and developing follicles, were recorded and measured. Maximum diameters were taken

of each corpus luteum and developing follicle. If fetuses or implantation sites were macroscopic, the entire reproductive tract was preserved in 10 percent formalin. Later, the fetuses were removed, sexed, weighed, and measured. Testes from 43 wolverines that appeared fresh were dissected free from the tunica vaginalis and fixed in 10 percent formalin. Histological sections were prepared from the body of each epididymis together with the underlying portion of the testis. The paired testes were weighed to the nearest 0.1 gram.

Age Determination

This study provided an opportunity to evaluate a number of techniques for age determination that are potentially useful for gaining insight into population parameters of wolverines. Until our study, these parameters had not been evaluated. The use of weights of *ossa bacula*, ossification of cranial sutures, and morphology of reproductive organs as indicators of age were discussed briefly by Wright and Ransch (1955). The use of eye lens weights as an indicator of age was mentioned by Friend (1968). A good correlation between layers of tooth cementum and two wolverines of known ages was reported by Myhre (1968). Materials evaluated for age determination in the present study included teeth, long bones, eye lenses, reproductive organs, and skulls. The techniques used in preparing the materials generally followed previously recorded procedures. Wolverine canines were sawed transversely at the gum line, the crown discarded, and the base decalcified in 5.7 percent nitric acid plus 1 percent formalin and 3 percent hydrochloric acid or 30 percent formic acid. All three reagents proved satisfactory. The decalcified roots were trimmed for a sagittal section through the labio-buccal axis. Sections were made at 16 to 30 microns on a freezing microtome; 20–22 microns seemed generally the most usable thickness. Sections were placed in fresh water and floated onto clean slides, blotted, dried for 10 to 15 minutes, stained in Paragon's multiple stain for frozen sections; the excess stain was drained, the slide was double-rinsed in fresh water to differentiate, removed from the water, and blotted dry. Sections were mounted in Permount, thinned with Xylene to a watery consistency. The sections were studied with a variable power binocular scope at 7× to 120×.

Eye lenses were processed in a way similar to that described by Friend (1968), with some exceptions. Repeated freezing and thawing, sometimes with 2 months between the death of the animal and fixation of the lens in 10 percent formaldehyde, created serious problems in collecting reliable material.

A well-fixed lens, after being dried in the oven, resembled a slightly flattened sphere, with a smooth surface; it was yellow in color. The oven-dried weight was 40–50 percent of the fixed, wet weight. Lenses that were exposed to prolonged periods of alternate freezing and thawing showed marked differences upon being dried. The surface was corrugated, the color was black, and the dry weight was less than 30 percent of the fixed, wet weight. All lenses that did not conform to the normal dried appearance were discarded.

Ossification of the epiphysis to the diaphysis of long bones has long been used as a criterion of age; examples are foxes (Sullivan and Haugen 1956) and wolves (Ransch 1962). We used the radius and ulna and in particular the junction of the distal epiphysis and diaphysis. The technique separates young-of-the-year from older animals but is useful only in species where ossification rates are known.

The weight and morphology of the os *baculum* have been used as criteria of age in a number of mustelids and other furbearers (Elder 1951 and many other authors). Wright and Ransch (1955) used os bacalum weights of wolverines to assist in establishing estimates of age. Ossa bacula used in this study were air-dried and weighed to the nearest 0.1 gram.

The morphology of female reproductive tracts has been used to differentiate sexually immature specimens from sexually mature animals (Ransch 1967). Some wolverines have their first young when 2 years old. Those animals trapped between November and March that possessed inactive ovaries and had short, thin-walled uterine horns were considered young-of-the-year. Uterine horns of nulliparous females older than 1 year were longer and thicker-walled than those of the younger females.

Wright and Coulter (1967) used ossification of cranial sutures to estimate the age of fishers (*Martes pennanti*), and Myhre (1968) used the technique for the wolverine. In our study, only the nasal and zygomatic sutures were considered in conjunction with the radius and ulna in our attempts to separate young-of-the year from older animals.

RESULTS

Breeding Biology

This study provided an opportunity to examine a reasonably large sample of reproductive tracts from male and female wolverines of several ages.

Wolverines are believed to breed in late spring and early summer (Wright and Ransch 1955, Danilov 1965, Pulliainen 1968) and to carry unimplanted blastocysts until the following winter. The only published records of breeding or parturition dates are those of Mohr (1938) and Davis (1967). Mohr stated that a pair of wolverines in the Copenhagen Zoo bred between July 17 and 22, 1916, and that the female gave birth to a litter on February 17, 1917. Davis (1967) reported that a female wolverine received at the Colorado Zoo on April 29 gave birth to two kits on February 16. The female was caged with a male, but the date of breeding was not determined. Aside from the authors cited, there has been considerable speculation about the breeding season of the wolverine (Makridin 1964, Pulliainen 1968). Most speculation seems to have been based on inadequate data or hearsay; however, it is difficult to obtain data on a furbearer that apparently does not breed during the trapping period. It proved difficult in this study as well, as only three adult wolverines were obtained for the critical May–June period—the months when some wolverines probably breed.

Table 3. Incidence of pregnancy in 247 wolverines collected in Alaska and the Yukon Territory, 1965 through 1968

Age	Age Class	Nonpregnant	Pregnant
0–15 months	0	109	0
16–28 months	1	20	20
29 months and older	2–13	8	90
Total		137	110*

* Includes 22 wolverines that had recently given birth.

Some female wolverines mature at about 1 year (probably at 15 months) and produce their first litters when they are 2 years old. The conclusion that only some of the 1-year-olds breed is based on cementum age determinations of 40 wolverines in age-class 1 (Table 3). Twenty of the animals were gravid or had recently borne young, and 20 showed no evidence of ovulation.

One difficulty in assessing past breeding performance of female wolverines was our inability to locate corpora albicantia. Wright and Ransch (1955) observed that corpora lutea of pregnancy in postpartum

Fig. 2. Wolverine ovary showing pediculated corpus luteum. Each segment of the scale equals 1 mm.

animals regressed rapidly, and our observations on a larger sample of postpartum animals agreed with their information. Many, though not all, of the corpora lutea of pregnancy are pediculated (Fig. 2). Corpora lutea that were not pediculated were invariably near the surface of the ovaries. The corpora lutea are the dominant features of the ovary, often measuring 3.5 × 4.0 mm or larger, whereas the ovary may measure only 9.5 × 11.4 mm. The ovaries of parous females frequently had white strands of tissue attached. These strands of material should not be confused with the fimbria associated with the oviduct. Though histological preparations were not made of these tissues, we suggest that they represent the corpora albicantia of regressed corpora lutea of pregnancy. Future workers utilizing freshly preserved specimens and refined histological techniques may find evidence of corpora albicantia, and they may also wish to analyze some of the tissue attached to the external surface of the ovaries.

Corpora lutea prior to nidation are small; the mean of two diameters of 49 corpora lutea from animals taken in November and December was 3.1 mm. Enlargement occurs during the gestation period, and the mean of two diameters of 60 corpora lutea from animals killed in January and February was 3.93 mm. Regression of corpora lutea after parturition is rapid—the mean of two diameters of 12 corpora lutea taken from three postpartum wolverines in March and April averaged 1.8 mm. Because corpora albicantia do not persist macroscopically, it was not possible, except prior to nidation, to distinguish accurately between females breeding for the first time and multiparous females. During the period prior to nidation, multiparous animals can be identified by the presence of placental scars. Counts of corpora lutea of females breeding for the first time and of multiparous animals showed no significant differences in the number of ova shed per estrous period.

The proestrous period was not well defined during this study. Ovaries from a number of parous and nulliparous females contained follicles of 1.5 to 2.5 mm in diameter during February, March, and early April. A lactating female killed in northern Alaska on April 12 contained follicles up to 1.7 mm in diameter, but her overall condition (the uterus had not regained normal size and shape after parturition) suggested that she was not in proestrus.

Two specimens collected on June 16 and June 28, respectively, showed developing follicles as bulges on the surface of the ovaries. Prominent pointed bulges were present on the surface of the ovaries of the animal collected on June 16. These were interpreted as representing a near-ovulation condition. No blastocysts could be recovered from the uterus. In both animals, the fixed uterine horns measured 6 mm in diameter. The uterine horns of immature animals at this time measured 3 mm in diameter and agreed with measurements made by Wright and Rausch (1955).

A specimen killed in the Yukon Territory on June 24 had recently conceived. Her ovaries contained three corpora lutea that measured approximately 2.5 × 2.8 mm each. Each corpus was composed of a layer of luteal cells about 0.8 mm thick, with a large undifferentiated fluid-filled lumen. Although the ovaries had desiccated considerably and further determinations were not possible, we judged that she had bred only a few days prior to capture. Two specimens also killed in the Yukon Territory on July 29 and August 30, respectively, were both pregnant, as indicated by the presence of three and four inactive corpora lutea, respectively. The corpora measured 2.9 × 2.7, 2.5 ×3.0, and 2.0 × 2.0 mm in the first animal and 2.1 × 2.0, 2.4 × 2.2, 2.1 × 2.1, and 2.3 × 1.9 in the second. Blastocysts or tubal morula were not found, but the oviduct was not serially sectioned.

Only about 50 percent of the Class 1 females had bred (Table 3). A Class 1 animal, collected on August 2 when she was approximately 16 months old, showed no evidence of sexual activity. Her ovaries were of normal adult size, but there was little follicular development. The uterine horns were thin but of adult length. This individual would not have produced a litter at 2 years of age unless the breeding season is rather extended, as is the case with some weasels (Enders 1952, Wright and Coulter 1967). The implantation and parturition pattern shown in Fig. 3 and the distribution of fetus sizes shown in Fig. 4 suggest a rather extended breeding season.

Nidation rarely occurs in December, as only 2 of 41 females killed in November and

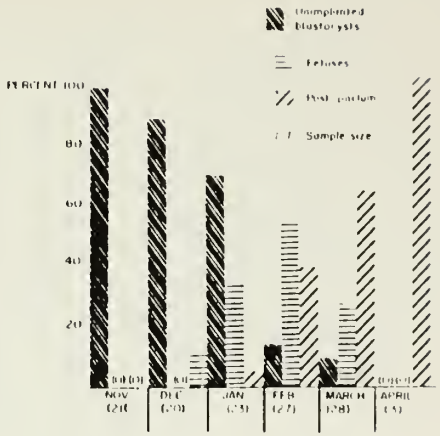

Fig. 3. Chronology of nidation and parturition in the wolverine.

December had macroscopic embryos or implant sites. One specimen reportedly killed on December 5 had fetuses of 19-mm crown–rump length. The kill date cannot be verified, but it is presumably correct. The uterus of a wolverine killed on December 15 contained implanted embryos.

Blastocysts were recovered from most of the animals killed in November and December. The number recovered frequently was fewer than the number of corpora lutea present. We believe that in using the flushing technique we lost or overlooked blastocysts. Decomposition of the reproductive tracts may also have contributed to loss of blastocysts.

Parturition commenced in January and continued through March, and in one case to mid-April; however, 61 percent (18 of 28) of the sexually mature females had given birth by the time they were captured in March. The capture dates are not intended to convey the impression that parturition was coincident with capture. Examination of the uterine horns and ovaries revealed that parturition had occurred

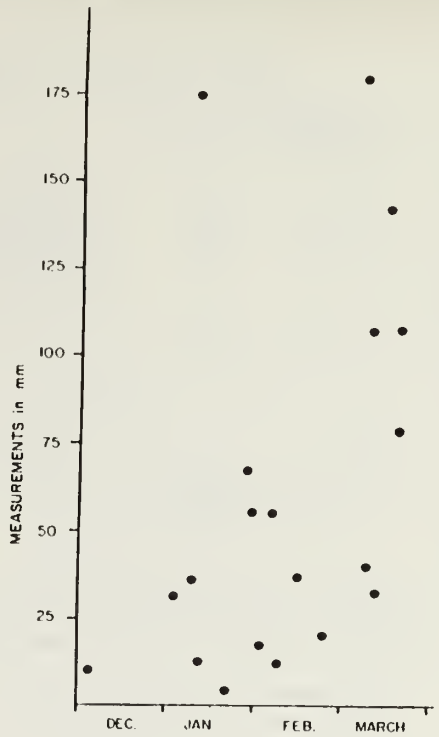

Fig. 4 Crown-rump measurements of wolverine embryos, Alaska

much earlier in some individuals. In some specimens, black placental scars had formed, uterine regression appeared complete, and corpora lutea of pregnancy had disappeared. The most obvious remaining sign of a recent pregnancy was the active mammary tissue. A few females showed evidence of having given birth recently, as the uterine horns were large (23-27 mm in diameter) at nidation sites, flaccid, and blood-engorged. In several instances, fragments of placenta were attached to the uterine wall. The stress of being trapped could induce parturition in near term females, but the only evidence of this was observed in a female killed in February that had injested one newborn; another was in the birth canal, and two more fetuses were in the right uterine horn. The size of these young suggested that birth might have been normal.

Our information suggested that in Alaska and the Yukon Territory most wolverines were born during the last half of February and the first half of March, though the period of parturition was spread over at least 2.5 months.

The period of active pregnancy, from nidation to parturition, was probably between 30 and 40 days. This estimate was largely based upon the observation that 50 percent of the females captured in February had implanted and 64 percent of those captured in March were postpartum. The earliest implantations were observed in a female killed December 5, and the earliest postpartum female was killed on January 15.

In addition to using female reproductive tracts to determine when female wolverine breed, implant, and give birth, we studied testes from males obtained in Alaska and the Yukon Territory for all seasons. Because some of the material available had undergone considerable autolysis, no attempt was made to utilize all the testes. Testes collected in late winter clearly showed an increase in weight (Fig. 5), spermatogenesis, and the presence of epididymal sperm. Most male wolverines were sexually mature at approximately 14 to 15 months, but some apparently did not produce sperm until they were 26 to 27 months old. The peak of breeding condition, as evidenced by testis weights and the presence of sperm in the epididymides, occurred in late May and June, but breeding probably occurred over a period of several months (Fig. 5).

Testes collected in the Yukon Territory in late July and August also suggested decreased testes activity, although a small

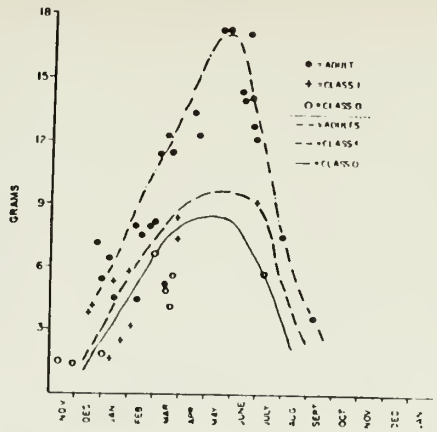

Fig. 5 Weights of 43 pairs of wolverine testes plotted against time

number of sperm were present in the epididymides. In addition, testis weights in the fall, although few were available, showed reduced size. Wolverine males definitely were not sexually active during late fall and winter.

Weights and measurements of *ossa bacula* suggested rapid growth of the *baculum* at about 1 year of age (Fig. 6). Two 1-year-old specimens showed active spermatogenesis, and sperm were found in their epididymides; however, another specimen collected in the Yukon Territory on July 10 showed no such development. Perhaps only a portion of the males were sexually mature by the breeding season of their second year. This generalized picture of breeding activity tended to substantiate an early summer breeding season.

The period of denning and denning habits were not extensively investigated during this study. Of three dens observed in Alaska, two were above timberline in snow-filled ravines. Carrion consisting of moose carcasses, which were in each instance located nearby, were intensively used. The third den was found in an abandoned

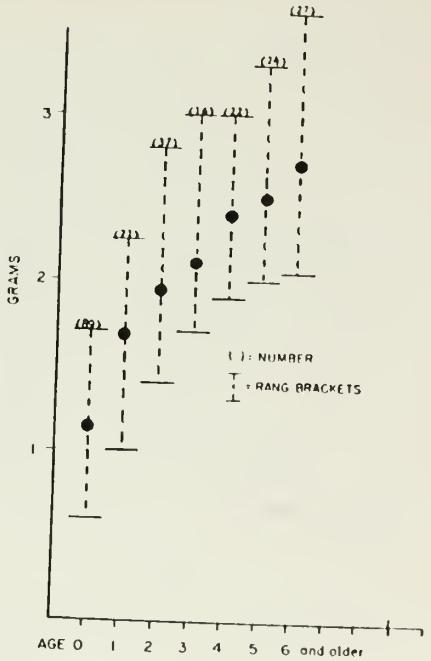

Fig. 6. Weights of 286 wolverine bacula compared with ages (in years) estimated by cementum

beaver house by trappers who excavated the den and killed the young on or about March 15. Pulliainen (1968) summarized the results of a number of studies concerned with wolverine litters found in dens (Table 4). Most of those dens were found by bounty hunters. Pulliainen stated that most dens were under the snow but on the surface of the ground. He further stated that selection of the den site was probably influenced by the facility with which the site could be adapted to a den. According to Pulliainen (1968), the young leave the den primarily in April and May.

Age Determination

In order to evaluate the various techniques for age determination, one had to be

Table 4. Size of wolverine litters in dens.[a]

	Size of Litters				Total Number of Litters	Mean Size of Litters
	1	2	3	4		
Finland						
Suvonen (1956)	1	20	22	2	45	2.6
Kroll (1959)	–	10	3	–	13	2.2
Pulkkinen (1963)	–	20	13	1	37	2.6
Pulkkinen (1968)	3	8	9	1	21	2.4
Sweden						
Zetterberg (1945)	1	18	17	2	38	2.5
Soviet Union						
Nasimovich (1948)	–	–	1	–	1	3.0
Panovkinkov (1960)	–	5	1	–	6	2.2
Total	5	81	66	9	161	2.5

[a] Taken from Pulkkinen (1968:414).

chosen as a base for the comparison. We chose the cementum deposition technique, because it has proved reliable on related species (Klevezal and Kleinenberg 1967) and because Myhre (1968) reported agreement between cementum layers and known age in two wolverines. The results of the age determinations, based upon layering in cementum, are presented in Table 5. The age-classes represent chronological periods: Class 0, 0–15 months, Class 1, 16–28 months; Class 2, 29–41 months, and on through the oldest class present in the sample. The technique is not without difficulties because it has not produced consistently readable sections; for example, cementum annulations were not always legible. In our experience, the annulations were not as distinct as were those of moose (*Alces alces*), lynx (*Lynx canadensis*), wolves (*Canis lupus*), or grizzly bears. The most consistent materials are for age-classes 0 and 1. Determination of these age-classes is further facilitated by the morphology of the canine tooth. Class 0 canines are characterized by an open root and a thin dentine layer with relatively little cementum. Class 1 is char-

Table 5. Age determinations based on cementum layers in canine teeth and sex composition of 923 wolverines, Alaska and the Yukon Territory, 1962–68.

Area and Sex Ratios	Age-class 0		1		2		3		4		5		6		7		8		9		10		11		12		13		Total	
	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
Area																														
Alaska[a]	32	52	27	21	10	8	3	8	3	8	3	9	4	9	2	5	1	7	0	0	1	2	0	1	0	1	0	1	88	135
Alaska[b]	136	106	76	36	54	12	16	9	19	14	19	20	5	2	11	7	7	11	0	5	1	1	0	0	2	2	0	0	344	210
Yukon	33	7	25	10	13	3	6	4	10	1	12	3	3	2	2	2	1	1	1	0	1	1	0	0	1	0	0	0	109	34
Total[b]	169	113	101	45	67	15	22	13	29	15	31	23	11	4	13	9	8	12	1	5	2	2	1	0	3	2	0	0	553	244
Sex Ratios																														
Alaska[b]	128:100		200:100		450:100		178:100		136:100 (Animals 5 years and older—100:100, 46 males and 48 females)																				164:100	
Yukon	150:100		210:100		447:100		169:100		193:100 (Animals 5 years and older—120:100, 70 males and 57 females)																				320:100	

[a] Data from 1965–66 and 1966–67, when only carcasses of male wolverines were purchased.
[b] Data from 1965–66 and 1966–67 are excluded.

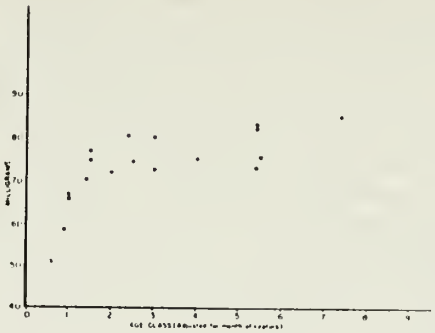

Fig. 7. Eye lens weights versus cementum layers, male wolverines, the Yukon Territory.

acterized by greatly increased layers of dentine, a closed root, a large pulp cavity foramen, and one distinct dark layer in the cementum bisecting two clear areas.

Based upon these criteria, wolverine teeth mature rapidly. Wright and Rausch (1955) found that deciduous teeth were still in place in July, but we found that a full complement of permanent dentition was present in a male taken on September 2 in the Yukon Territory. The sequence of tooth eruption is not known.

The weights of oven-dried lenses are plotted against age as determined from cementum annulations in Figs. 7 and 8. The material collected in Alaska (Fig. 8) showed some indication of increased weight with age. However, the large variation within a single age-class caused an overlap between years so that the material was unsuitable for determining age. This sample was collected entirely from trappers, and the lenses were exposed to many different conditions, all of which would affect the weight (Friend 1967).

Most of the lenses used from the Yukon Territory were collected from freshly killed specimens and were fixed immediately in 10 percent formalin. Although those data showed better correlation with age, after

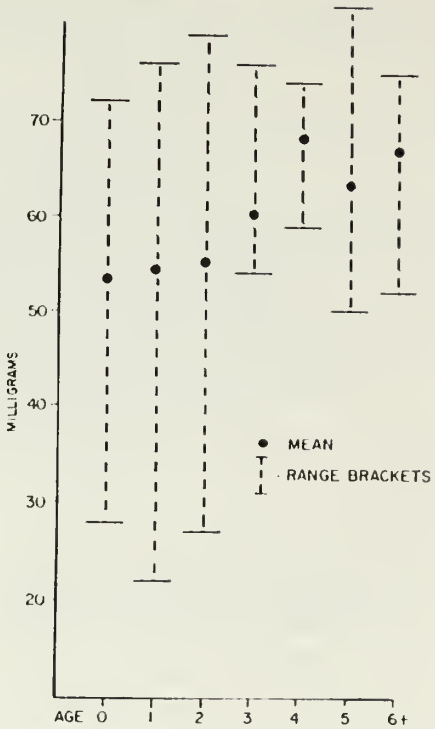

Fig. 8. Mean and range of 101 wolverine lenses plotted against cementum annulations, Alaska.

the first year, the rate of growth of the lens was so slow that different age-classes could not be separated. A larger sample is necessary before it can be positively stated that lens weight will separate young animals from adults. It appears that a lens weighing less than 70 mg dry weight represented a young animal. Other workers have found that in carnivores the lens technique will separate juveniles from adults (Lord 1961, Sanderson 1961, Friend and Linhart 1964).

The skeleton of a wolverine develops rapidly for an animal of its size. The fact that long bone epiphyseal junctions apparently are closed by 9 to 10 months of age

Table 6. Age composition based upon ossification of long bones and skull sutures.[a]

	Number						
	Age-class 0		Age-class 1		Older Than Age-class 1		
Season	Total	Aged Incorrectly[b]	Total	Aged Incorrectly[c]	Total	Aged Incorrectly[c]	Aged as Adult
1967–68	60	3	29	6	48	2	46
1966–67	19	9	29	4	44	2	42
1965–66	31	3	17	6	41	3	41
1964–65	52	7	15	5	24	3	21
1963–64	37	4	19	4	35	4	31
1962–63	36	1	28	10	34	2	32
1961–62	35	0	19	11	24	4	20
Total[d]	303	27	156	46	253	20	232

[a] Age as determined by cementum layers is assumed to be correct.
[b] Placed in an older age-class.
[c] Placed in Age-class 0.
[d] Total sample = 712. Based on layers of cementum, there were 303 kits and 409 subadults and adults (43 percent kits and 57 percent adults). Based on closure of epiphyses and cranial sutures, there were 343 kits and 369 adults (48 percent kits and 52 percent adults).

reduces the value of the radius and ulna in identifying young-of-the-year. Young and old wolverines caught in November and early December could generally be separated by the degree of fusion of the epiphysis, as the epiphyseal junction in young animals was either open or recently fused.

Weights of ossa baculi proved sensitive to age when compared with age determinations by the cementum (Fig. 6). There was some overlap, between Class 0 and Class 1 individuals, which could be reduced by eliminating Class 0 animals killed in March and April, when they were approximately 12 to 14 months old. As was shown earlier, some Class 0 males reached sexual maturity during that period. The overlap in weights of baculi occurred because the growth of the os baculum is stimulated by male hormones (Wright 1950) at the onset of sexual activity. Development of the os baculum apparently continued thereafter, because the means indicated an increase in weight with age. The utility of this technique probably does not extend beyond separating young-of-the-year from older animals. Although easier and less expensive than the cementum technique, and more accurate than the long bone-cranial ossification technique, the os baculum is probably not worthwhile for future studies. Anyone with access to a large collection of ossa baculi weights will probably have access to material for the cementum deposition technique.

The use of certain cranial sutures to estimate ages of wolverines was proposed by Wright and Rausch (1955). In the present study, the internasal and zygomatic sutures proved the most useful, and even these exhibited considerable variation. In an effort to minimize error, the long-bone technique was combined with the use of cranial sutures to estimate the ages of 303 Class 0 animals and 409 older animals (Table 6). Twenty-seven Class 0 individuals were incorrectly placed in an older age-class, and 46 of 156 teeth in cementum Class 1 were classified as Class 0 (Table 6). In part, the fact that cementum Age-class 0, as used here, included a fair proportion of animals just at 1 year or slightly older is responsible for some of the confusion between age-classes 0 and 1. Those animals were approaching sexual maturity, and all of the sutures and epiphyses were closed, and some of the first cemental layer was being

deposited. It is extremely difficult to separate Class 0 from Class 1 individuals during this period of skeletal and sexual maturity.

Of the six techniques tested for age determination, only cementum deposition provided a reliable estimate of age beyond 1 year, and it is therefore potentially useful in further analyzing the population age structure of wolverines. Reproductive organs, long bones, and cranial sutures provided an adequate separation of young-of-the-year from older animals only if those young less than 10–11 months were considered. The validity of the chronological assignments, based upon the cementum deposition, must await verification through acquisition of known age specimens. There is little likelihood of these data becoming available soon, because only limited studies are continuing in Canada and there are none in Alaska. In Russia, where wolverine populations are still abundant regionally, there seems to be more interest in eliminating the animal than in doing research on it (Makridin 1964). We believe that the chronological assignments are essentially correct and can be improved upon by refinement of the techniques employed.

Sex and Age Composition

Apparently little information on the sex composition of wolverine populations is available. Pulliainen (1968) found 15 males and 22 females in 37 kits taken from dens. The sex ratio of these animals was not significantly different from a 1:1 ratio ($\chi^2 = 1.324$). The sex ratio of 14 fetuses obtained during this study was six males and eight females.

Sex ratios derived from catch statistics often do not accurately reflect the ratio existing in the population. Yeager (1950) postulated that this disparity in the pine marten (*Martes caurina*), which is usually biased toward males, results from the tendency of males to travel over larger areas than females. The data from Alaska, where most of the animals were trapped or snared (Table 2), show a male:female ratio of 164:100 in a sample of 554 animals (Table 5). We suspect that males were represented disproportionately and that variation in sizes of home ranges accounted for part or all of the difference.

Analysis of the sex components of the catch by age-class revealed an unusual distribution of sex ratios by age-classes (Table 5). In kits (Age-class 0), males outnumbered females by only 128:100, but in Age-classes 1, 2, and 3, the ratios were 200:100, 450:100, and 178:100, respectively. A combination of Age-classes 5 through 13 revealed a ratio of 100:100. The unexpected disparity of sex ratios in the age-classes comprising the majority of the sample, particularly in Age-classes 1, 2, and 3, cannot be explained satisfactorily. Perhaps kits had not established territories of their own, and the nearly equal representation of both sexes in the catch reflected this. The dramatic changes in age-classes 1, 2, and 3 may merely reflect the tendency of males to roam over greater areas. The even sex ratio among the older age-classes may reflect a reduction of males through exploitation.

The denning habits of wolverines, as described by Pulliainen (1968), argue somewhat against our interpretation. His own work and that of other authors indicated that male wolverines visit den sites and may play a role in rearing the young. If those observations are correct, the home range of males, for the purpose of interpreting differences in sex ratios of trapped wolverines, cannot be considered entirely different from that of the female. It is possible that the male's interest in the den is not associated with caring for the young, as recrudescence of the testes commences in late winter.

Table 7 Indicators of productivity in wolverines.

Year	Placental Scars		Corpora Lutea		Fetuses	
	Mean	Sample Size	Mean	Sample Size	Mean	Sample Size
1962	3.3	10	5.0	1	2.6	5
1963	3.7	3	4.0	1	3.8	6
1964	2.6	5	–	–	3.7	7
1965	3.5	8	3.5	20	2.7	7
1966	3.1	29	3.1	37	5.2	5
1967	3.9	30	3.6	42	3.4	19
1968	2.9	14	3.0	20	3.6	5
Total	3.4	99	3.4	121	3.5	51

Therefore, the presence of males at den sites may represent their annual search for females in estrus.

If wolverines are monogamous, even seasonally, a harvest biased toward males could seriously reduce reproduction; however, we suspect that they are polygamous and that the presence of males at den sites represents either a renewed interest in females or the casual happening upon a site that might provide food. Although the matter needs further study, obtaining meaningful information on the movements of wolverines will require the expenditure of considerable resources.

Productivity

Pulliainen (1968) published a summary of data on litter sizes obtained from Finland, Sweden, and the Soviet Union (Table 4), but productivity of wolverines as a species or of individual populations has not been studied extensively.

The present study provided considerable direct and indirect information on the productivity of wolverines (Tables 3 and 7). Analysis of uterine contents from 54 wolverines that had detectable fetuses showed an average of 3.5 embryos or fetuses per pregnancy. The frequency distribution of litters *in utero* is shown in Fig. 9. Observation of 121 females showed an average of

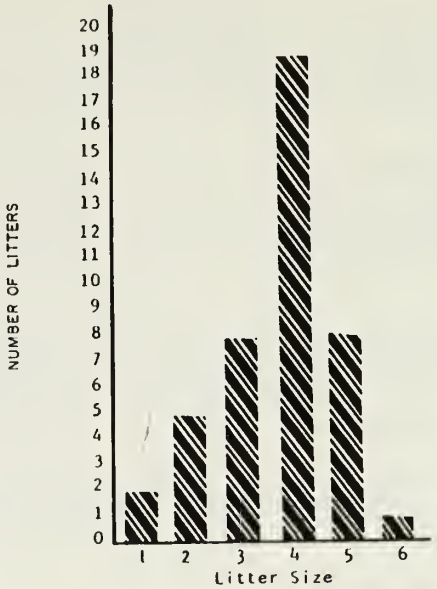

Fig. 9 Frequency histogram of 42 wolverine litters (in utero).

3.4 corpora lutea of pregnancy, and an average of 3.4 placental scars were found in 99 females. Because placental scars may persist for more than one pregnancy, and because discrimination between scars of the immediate past pregnancy and earlier pregnancies is somewhat subjective, only the distinct scars were used. Some previous workers had difficulty distinguishing placental scars in preserved specimens; to avoid this problem, the scars in our study were counted prior to fixing, at which time they were obvious (Fig. 10).

The data on age composition provided another means for estimating productivity. The figures for age composition could be considered net productivity, since they represented the proportion of young that survived to harvestable age.

In a sample of 380 female wolverines

(Table 5), there were 165 in Class 0, 69 in Class 1, and 131 in Classes 2 and older. If mortality was constant within all age classes, and if the population was not rapidly increasing or decreasing, then the 163 females in Age-class 2 and older produced the 165 females in Age-class 0. If the true sex ratio is 100:100, there would be a total of 330 kits produced by the 163 females, disregarding the few that do not breed. This equals 2.02 kits per female. This is about 1.5 kits less per female than is indicated by the *in utero* data (Table 7) and is a reasonable difference, since mortality factors had been in operation for nearly a year.

Body Weights and Measurements

The weights and measurements of the skinned carcasses from 183 wolverines from Alaska and of whole carcasses of 101 wolverines from the Yukon Territory are presented in Table 8. In order to compare these weights, we estimated that the hide, blood loss, and desiccation equaled 25 percent of an animal's total weight (Myhre 1968). Skins from 14 animals killed in the Yukon Territory averaged 18.6 percent of the skinned weights, with a range of 15.7 to 23.0 percent. Skinned carcasses of four wolverines from Alaska that had desiccated slightly averaged 75 percent of the whole weight. The whole weights of six male wolverines from Alaska averaged 32 pounds, with a range from 29 to 37 pounds. Two females weighed 21 and 22 pounds, respectively.

Myhre (1968) gave the mean weight for 51 males as 14.6 kg (32.1 lb) and for 39 females as 9.9 kg (21.8 lb). The means of skinned weights were 11.7 ± 0.2 kg (25.7 ± 0.4 lb) and 7.9 ± 0.2 kg (17.4 ± 0.4 lb), respectively.

Pulliainen (1968) gave the mean weight of eight adult females as 12 ± 0.5 kg (26.4 ± 1.1 lb) and the mean weight of 20 imaged

Fig. 10 Placental scar in a wolverine. The dark central area often was of a bright red pigment. 8×

females shot in winter as 11 ± 0.6 kg (23.2 ± 1.3 lb). Makridin (1964) stated that some males weighed 17 kg (37.4 lb) and that males from Yamal averaged 14 kg (30.8 lb), which was about 2 kg (4.4 lb) heavier than those caught in the region of the Pechora-Hydeganne reserve. Rausch (1953) gave the weight of the largest male he weighed as 17.48 kg (38.5 lb). The weights presented in Table 8 generally concurred with the weights that have been reported previously, although the largest male weighed 34 pounds skinned, or approximately 45 pounds whole, which exceeded previously reported weights for wolverines.

Young wolverines must grow quickly during the first year. One young male captured on September 2 weighed 15 pounds.

Table 8. Weights and measurements of 284 skinned and 101 whole wolverines taken during winter in Alaska and the Yukon Territory, respectively.

Sex, Age and Area	Weights (lb)			Measurements (cm)								
				Hind Foot			Height at Shoulder Without Toenail			Total Length (straight line)		
	Mean	Range	Number	Mean	Range	Number	Mean	Range	Number	Mean	Range	Number
Male												
Adults												
Alaska	22.7	16.5–31.0	61	15.5	12.0–18.0	45	41.5	31–46	40	92.4	85.0–100.0	56
Yukon	31.2	26.2–36.3	52	18.7	16.9–20.5	52	–	–	–	100.6	90.1–111.6	51
Kits												
Alaska	21.1	13.5–26.5	33	15.9	13.0–19.0	26	40.5	37–44	21	90.7	87.0–98.0	31
Yukon	29.1	20.7–37.2	19	18.6	17.0–20.5	21	–	–	–	98.5	90.1–108.5	21
Female												
Adults												
Alaska	15.5	12.0–18.5	50	14.0	13.0–17.0	46	38.6	33–42	30	81.7	79.0–91.0	49
Yukon	20.7	18.4–23.7	21	17.1	16.0–18.3	21	–	–	–	91.2	84.8–98.0	21
Kits												
Alaska	15.4	12.0–19.5	39	14.2	13.0–17.0	33	38.0	29–42	29	83.1	79.0–90.0	37
Yukon	20.1	18.0–22.6	7	16.8	16.2–17.4	7	–	–	–	87.8	82.4–91.9	7

Sex, Age and Area	Total Length (contour)			Girth			Tail		
	Mean	Range	Number	Mean	Range	Number	Mean	Range	Number
Male									
Adults									
Alaska	103.0	93–111	55	39.7	32–48	60	20.7	17.0–23.0	56
Yukon	–	–	–	–	–	–	20.8	16.0–23.4	51
Kits									
Alaska	101.3	92–112	32	39.3	30–45	31	20.1	17.0–24.0	33
Yukon	–	–	–	–	–	–	20.3	15.6–24.1	20
Female									
Adults									
Alaska	92.9	76–101	47	33.8	29–41	50	19.1	15.0–23.0	46
Yukon	–	–	–	–	–	–	19.7	16.2–23.4	21
Kits									
Alaska	92.9	88–100	37	34.1	29–43	38	18.7	16.0–21.0	37
Yukon	–	–	–	–	–	–	18.6	16.7–21.5	7

Other animals taken in the early winter (November–December) had reached adult size. The differences in weights between Class 0 animals and adults shown in Table 8 were not significant. Only animals taken during the winter period were used in the preparation of that table.

The measurements of the hind foot and height at shoulder taken from skinned carcasses (Table 8) were not comparable to similar measurements on whole animals because the toenails were not present.

Condition

The extent of body fat deposition and particularly the kidney index (weight of kidney fat/weight of kidney × 100) has been shown to be a sensitive indicator of

Table 9. Comparison of kidney indices (weight of kidney fat/weight of kidney × 100) for 61 wolverines collected in the Yukon Territory.

Season	Males			Females		
	Number	Mean	Range	Number	Mean	Range
October–February (winter)	7	24.8	9.9–53.5	5	31.9	13.4–69.9
March–April (spring)	27	31.9	9.0–95.0	13	30.2	14.4–65.4
May–September (summer)	6	15.4	5.5–30.5	3	18.3	8.8–28.3

the condition of an animal (Riney 1955). During 1967, 61 wolverine carcasses from the Yukon Territory were processed according to the technique of Riney to obtain values for kidney indices. The results are presented in Table 9.

In this sample, no significant differences were found between males and females, when compared for the three seasonal categories. There was an indication that females were in better condition than males during the winter, but the difference was not significant with the small sample size.

At the 10 percent level of significance, there is a difference between the summer index and the spring index in males (t = 2.03, df = 31). The index in females also shows a decrease in the summer, but it is not significant statistically (t = 1.22; df = 14).

The available data (Table 9) indicate that the period during which snow is on the ground, and particularly the early spring, provides the best sustenance for wolverines. If the reproductive cycle is so timed that the young are born during the period of the most abundant food supply, the timing of the reproductive cycle of the wolverine supports the hypothesis that early spring is the most favorable time of the year for the wolverine.

The general physical appearance of the wolverine in the summer is much poorer than its appearance in winter. Not only is the animal lacking body fat in summer, but the coat is shedding and unprime. Observations of wolverines on high alpine snow patches during the heat of summer indicate that thermal stress may be of considerable importance to the well-being of the species.

Foods

The food habits of wolverines in Fennoscandia and parts of Russia have been reported by Pulliainen (1965) and Makridin (1964), respectively. They consider the wolverine an effective predator of domestic reindeer (*Rangifer tarandus*). Makridin (1964) reported that hoofed mammals are an important part of the diet of wolverines and that they successfully attack moose. He also stated that they rob traplines, eating and mutilating valuable furbearers, particularly the arctic fox (*Alopex lagopus*). Rausch (1959) reported the occurrence of food items from 20 stomachs as follows: moose or caribou (*Rangifer tarandus*), 12 (60 percent); and porcupine (*Erethizon dorsatum*), 3 (15 percent). Additional items included *Microtus* sp. and ground squirrel (*Citellus spermophilus*)—both from a specimen killed in the summer—snowshoe rabbit (*Lepus americanus*); northern red-backed mouse (*Clethrionomys rutilus*); magpie (*Pica pica*); unidentified hawk; unidentified bird; and remains of fish. He believed that the moose and caribou were probably carrion.

The information presented in Table 10 is largely from animals that were trapped or snared. Most of the digestive tracts were empty or contained only debris such as bits of wood, grass, soil, and portions of wolverine feet. Those that contained identifi-

Table 10. Occurence of food items in stomachs and colons from 193 wolverines from Alaska.

Moose	Caribou	Hare	Fish	Bird	Microtine	Beaver	Unidentified Flesh	Empty	Trap Debris	Others*
27	17	23	3	3	8	2	6	99	42	2

* Portions of a lynx in one specimen and 190 grams of blueberries in a specimen collected in September.

able material probably were killed shortly after capture, but we cannot rule out the possibility that some of the items were bait.

The materials found in wolverine digestive tracts during this study, and our field observations, reveal that wolverines eat a large amount of carrion. We observed them feeding on moose and caribou that were killed by wolves and hunters and some that apparently succumbed from natural causes. In coastal Alaska, unidentified whales, walrus (*Odobenus rosmarus*), and seals that wash ashore are used extensively by wolverines for food.

The summer foods are not well known, but microtines, ground squirrels, and marmots (*Marmota caligata*) are utilized. A wolverine shot in September contained five microtines weighing 153 grams plus 190 grams of blueberries (*Vaccinium uliginosum*). The entire digestive tract of this animal was stained dark blue, and apparently it had been utilizing blueberries regularly. A wolverine killed in midwinter had a porcupine quill encapsulated in its viscera; one end of the quill had penetrated the left ovary. In another instance, a massive infection of the sternum was attributed to several quills embedded in the overlying muscle tissue. Rausch (1959) also reported finding porcupine remnants in wolverine stomachs.

Our observations and general impressions were that wolverines were capable of capturing prey, but they used carrion extensively if it was available. Berries were used seasonally. Although wolverines can kill domestic reindeer and wild ungulates if the latter are under unusual environmental stress, such predation probably is not significant, even though observations reported from Fennoscandia and Russia contradict this viewpoint.

Management Implications

The records of past harvests of wolverines in Alaska, prior to the initiation of a bounty in 1953, were gathered from a mandatory report required of each fur dealer and from export permits required whenever a wolverine skin was shipped from Alaska (Table 1). A bounty of $15.00 was paid for each wolverine legally killed during the period 1953 through 1968. In 1968, the state legislature enacted a law that transferred the authority for establishing bounties to the Board of Fish and Game. The Board promptly eliminated the bounty. The information on annual harvests of wolverines obtained from these various sources are not directly comparable. They do, however, provide a general estimate of long-term population trends, as evidenced by estimates of annual harvests.

The records revealed several periods of high and low harvests, with amplitudes exceeding 300 percent. There are four periods of greater-than-average harvests—1918–20, 1927–29, 1947–50, and 1964–68.

Yield was not always indicative of population abundance, and trapping effort and techniques were influenced by a host of variables not necessarily related to the abundance of a species. For example, trappers in interior Alaska were very active in the middle 1960's, when lynx were abundant and commanding a good price. Wolverines undoubtedly were subjected to additional pressure in Game Management Units 11, 12, 13, and 20 during this period. The increasing popularity of hunting wolves from aircraft has probably also contributed to the harvest of wolverines in Alaska, although it is illegal to shoot them from an airplane.

Although all records of past harvests suggested that wolverine numbers showed periodic fluctuations, these fluctuations apparently were common both before and after the bounty was authorized. Lensink (1958) suggested that the bounty was not a sufficient stimulus to induce additional trapping pressure. Harvest records obtained subsequent to Lensink's study tended to substantiate his views.

The future of the species is reasonably secure in Alaska. At present, the wolverine is classified as a big game animal and as a furbearer. Earlier management practices had provided some protection to the species, with aerial hunting and trapping during the summer months eliminated. Early in 1960, concurrent with the transfer of management authority over wildlife to the state, wolf control activities by the federal government were terminated in most of the state. This program was primarily aimed at wolves, and strychnine and cyanide were used extensively. Wolverines, because of their proclivity for carrion, were particularly susceptible to those nonselective control techniques.

In the Yukon, the wolverine is classed as a predator and as a furbearer. Anyone owning a valid hunting license could legally shoot wolverines as predators. As a furbearer, it could be trapped by a person owning a general hunting license and possessing a registered trapline. In addition, the Yukon is becoming a favorite source of supply for live animals required by zoological gardens and research institutes.

In the Yukon, for the past 6 years, the annual harvest attributable to all sources, including animals killed at predator control bait stations, has averaged about 150 animals. Variations during that period do not appear significant, but, if anything, the total take has been decreasing. Decreased use of strychnine in the past 2 years and decreased trapper activity have been partially offset by the increased take of live animals and the increased harvest by trophy hunters. The status of the species in the Yukon Territory seems secure for the immediate future.

The trapping season in both Alaska and the Yukon Territory extends from early November until mid-April. Pelts are commanding a high price ($50.00–$75.00) on the fur market, and even better prices are obtained locally for garment trim and rug mounts. Live animals are being sold to wild animal entrepreneurs for about $200.00.

Habitat changes that could significantly affect the wolverine over a large portion of its range are not likely to happen in the near future in Alaska or the Yukon Territory. The impact of hunting from tracked vehicles cannot yet be assessed, but it is a potential problem on the tundra areas. Regulation of this type of hunting will be necessary. The scavenging nature of the wolverine will probably bring the animal into contact with exploration camps and lead to the killing of additional animals. More attention to disposal of refuse around field camps, garbage dumps placed farther from living quarters, and strict regulation of the use of firearms in camps will minimize the kill from the expected increase in field activities.

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HOME RANGE AND HABITAT USE BY WOLVERINES IN SOUTHCENTRAL ALASKA

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Abstract: A wolverine (*Gulo gulo*) population was studied in the Susitna Basin of southcentral Alaska from 1980 to 1983. Based on logarithmic extrapolations, annual home range sizes were estimated at 535 and 105 km² for males and postpartus females, respectively. Wolverines utilized significantly different ($P < 0.05$) elevational strata during different seasons ($\bar{x}$ = 1,043 and 818 m for Apr–Oct and Nov–Mar, respectively), probably in response to differences in prey distribution and abundance. Habitat analyses showed an avoidance of forest types in summer and tundra types in winter.

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The wolverine, the largest terrestrial mustelid, has a circumboreal distribution and a valuable pelt. Because wolverine population densities are naturally low and the elusive animals occupy remote habitats, few studies have been conducted. This paper describes home range, movements, and habitat use by wolverines in southcentral Alaska.

This study was supported by the Alaska Power Authority and the Alaska Dep. Fish and Game (ADFG). Appreciation is expressed to ADFG employees S. R. Peterson and R. J. Tobey for reviewing early drafts of the manuscript. E. A. Goodwin provided critical lab time and support. S. M. Miller provided statistical support. K. Z. Adler handled typing and bookkeeping throughout the project. Pilots V. and C. Lofstedt, H. C. McMahan, and A. and J. Lee participated in the field aspects of the project.

STUDY AREA AND METHODS

The study was conducted in a 7,700-km² portion of the upper Susitna River Basin in southcentral Alaska. Characteristics of the habitat have been described previously by Skoog (1968). Elevations range from 260 to 2,200 m. Low elevations are dominated by spruce (*Picea* spp.) forests, with a shrub and deciduous transition zone blending to tundra and shrub birch (*Betula* spp.) habitat types at higher elevations.

From 1980 to 1983, 22 wolverines were captured, radiocollared (Ballard et al. 1982), and tracked from fixed-wing aircraft. Wolverines were subjectively aged based on tooth wear patterns and degree of maturation of reproductive organs. Radio transmitters (Telonics, Inc., Mesa, Ariz.) were enclosed in metal canisters, and the transmitter-to-antenna connection was encased in urethane. Collar webbing was made of butyl rubber with an internal stainless steel whip antenna. The entire radio-collar package weighed 430 g.

Wolverine locations were gathered whenever weather and daylight permitted and were plotted on 1:63,360-scale U.S. Geological Survey topographic maps. The following data were recorded: date, time, activity, association, elevation, aspect, slope, and associated habitat type (Viereck and Dyrness 1980). Availability of habitat to the animals was determined by recording the habitat type at each section corner of the mapped study area (McKendrick et al. 1982). Use of habitat was determined by plotting all wolverine locations that were within the mapped area (N = 178) and tallying corresponding types. Statistical comparisons between availability and use were determined by a standard F-test. Logarithmic transformations based on the relationships between the number of locations and cumulative home range size were used to project annual home range sizes.

RESULTS AND DISCUSSION

From April 1980 to November 1983, length of contact with instrumented wolverines ranged from 1 to 426 days ($\bar{x}$ = 147). A total of 258 point locations was gathered. Mortality (N = 10) and suspected transmitter failure (N = 7) were the primary reasons for loss of contact. In 1983, transmitters were redesigned to reduce failure.

Home Range

The relationship between number of locations and home range size was examined (Fig. 1) and used to estimate total annual home range

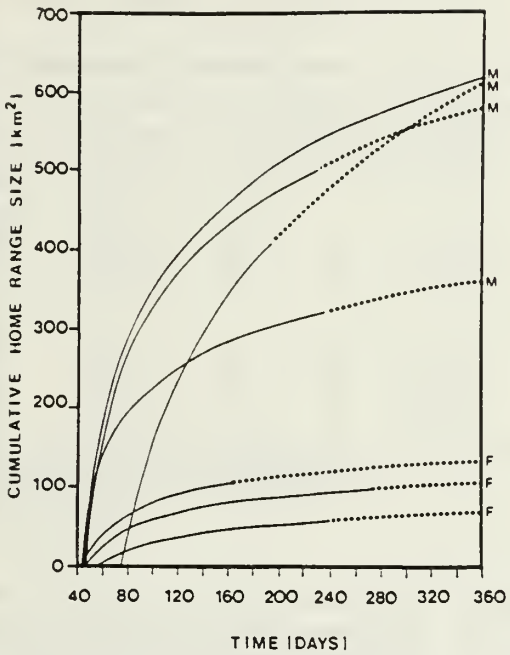

Fig. 1. Logarithmic curve analysis of home ranges of 4 male (M) and 3 female (F) wolvennes instrumented in the middle Susitna River Basin, southcentral Alaska, based on cumulative use of the home range during radio tracking, 1980–83. Solid lines indicate the log curve based upon collected data, and dotted lines are extrapolations based upon the collected data.

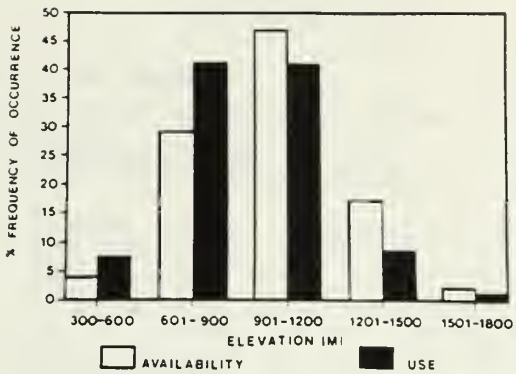

Fig. 2. Availability vs. use of various 300-m elevational strata by 22 instrumented wolvennes in the middle Susitna River Basin, southcentral Alaska, 1980–83.

of each wolverine. Inadequate sample sizes or infrequent contact allowed use of only 7 of our 22 instrumented wolverines for the home range analysis. This sample consisted of 4 males and 3 females although data from all wolverines were used for other habitat analyses.

Similar to other mustelids (Harestad and Bunnell 1979, Melquist et al. 1981, Messick and Hornocker 1981, Whitman 1981), wolverine males had larger ($F = 261$, $P < 0.01$) home ranges (535 km²) than females (105 km²). All females had kits during most of the monitoring period, which probably affected seasonal home range size. Magoun (1982) suggested that postpartus females in northwest Alaska may have smaller home ranges than unaccompanied females because of site attentiveness to dens where young are reared. Similarly, in our study an unaccompanied adult female, which had too few locations for home range analysis, utilized an area almost 3× greater (290 km²) than the average home range size of the postpartus females.

Home range sizes of Montana wolverines averaged 422 km² for males and 100 km² for lactating females in spring and summer (Hornocker and Hash 1981). Our larger estimates may be due to differences in productivity of the habitat (Harestad and Bunnell 1979) or differences in sampling and analyses. Because our estimates of average home range size of females were calculated for an entire year, no comparison with the Montana spring and summer females was possible. Both the Montana (Koehler et al. 1980, Hornocker and Hash 1981) and the northwestern Alaska (Magoun 1982) studies indicate that home ranges of sexes overlap. Our data support these results.

Both marten (*Martes americana*) and mink (*Mustela vison*) generally increase their home range in winter (Harestad and Bunnell 1979). Because wolverines seasonally utilize different segments of their annual home range, it appears that their home range expands in winter. However, 2 partially overlapping seasonal home ranges were used in summer and winter, giving the impression that the home range expanded in winter. Actually, there was no significant difference ($P > 0.05$) in size between the summer range and the winter range; they simply encompassed different, but overlapping, areas.

Elevation

Relocation data suggested that wolverines move to higher elevations in summer (Apr–Oct) and to lower elevations in winter (Nov–Mar) ($\bar{x} = 1{,}043$ and 818 m, respectively; $P < 0.05$). There were no differences ($P > 0.05$) between the sexes in seasonal elevational use.

These elevational changes between seasons probably are induced by changes in prey dis-

Table 1. Seasonal use of 4 broad habitat types by wolverines in southcentral Alaska, 1981–84.

Habitat type	Proportion of total area	*N* observations	*N* observations expected	Proportion of observations in each area	CL on proportion of occurrence (90% family confidence coefficient)	Selection
Winter						
Tundra[a]	0.218	6	12	0.109	$0.015 \le P_1 \le 0.203$	Avoided
Shrub[b]	0.412	21	23	0.382	$0.235 \le P_2 \le 0.529$	
Forest[c]	0.326	26	18	0.473	$0.322 \le P_3 \le 0.624$	
Other[d]	0.038	2	2	0.036	$-0.020 \le P_4 \le 0.092$	
Summer						
Tundra	0.218	32	26	0.271	$0.179 \le P_1 \le 0.363$	
Shrub	0.412	52	49	0.441	$0.339 \le P_2 \le 0.543$	
Forest	0.326	28	39	0.237	$0.149 \le P_3 \le 0.325$	Avoided
Other	0.038	6	4	0.051	$0.006 \le P_4 \le 0.096$	

[a] Includes both mat-cushion tundra and sedge-grass tundra.
[b] Includes shrub birch, willow (*Salix* spp.), and alder (*Alnus* spp.) types.
[c] Includes spruce, mixed, and deciduous forest types.
[d] Includes both rocks and ice

tribution and abundance (van Zyll de Jong 1975; Gardner and Ballard 1982; Whitman and Ballard 1983, 1984). During summer at higher elevations, arctic ground squirrels (*Spermophilus parryii*) and other small mammals and ground-nesting birds are plentiful (Kessel et al. 1982) and probably constituted much of the spring and summer diet. Hibernation and migration of prey species combined to reduce availability at high elevations during winter. In response, wolverines moved to lower elevations where they fed primarily on moose (*Alces alces*) and caribou (*Rangifer tarandus*) carcasses resulting from gray wolf (*Canis lupus*) kills and starvation (Fig. 2).

Habitat Use

Analyses indicated that wolverine habitat use varied seasonally (Table 1). Although no specific habitat types were preferred for either the summer or winter period, certain types were avoided (Neu et al. 1974). In summer (Apr–Oct), forest types were avoided. Shrub, tundra, and rock-ice types were used according to their availability. During winter (Nov–Mar), tundra types were avoided, whereas forest, shrub, and rock-ice areas were utilized in proportion to their availability.

Viable wolverine populations still exist throughout most of Alaska. This is undoubtedly due to sparse human populations and the wolverine's use of rugged and relatively inaccessible habitats. As land-use practices change with the expanding human population, management of wolverines will need to become more intense if populations are to remain harvestable.

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REPRODUCTION IN THE WOLVERINE, *GULO GULO*

By Philip L. Wright and Robert Rausch

The reproductive habits of the wolverine, largest of the terrestrial mustelids, have remained largely unknown. In the American literature there are scattered statements indicating that the young are born in the spring and that the number of young at birth is from two to four (Seton, 1927). Seton also states that mating takes place in March and the young are born in June. These statements, which are only partially correct, have come largely from woodsmen who have made no detailed study of the species. Mohr (1938, 1939) states that breeding occurred between July 17 and 22, 1915, in a pair of captive European wolverines kept at the Copenhagen Zoo and the female gave birth to a litter on February 17, 1916. The same female produced another litter on February 24, 1917 after breeding the previous summer. She suggests that the European wolverine has a gestation period of about nine months. Recently Rausch (1953) has concluded that the American and European wolverines belong to the same species (*Gulo gulo*). The above evidence and the known occurrence of delayed implantation with the accompanying long periods of gestation in several mustelids suggest that this species should be more thoroughly investigated.

The collection of Alaskan mammals carried on under the direction of the junior author since January, 1949, is an important activity of the Animal-borne Disease Branch of the Arctic Health Research Center. The material thus far obtained has been utilized for studies of diseases and helminth parasites, and has provided information of interest to mammalogists. In the course of these collections Rausch obtained several wolverines in 1949 and 1950 and some female reproductive tracts were sent to Wright for study.

In species in which breeding occurs in mid-summer and the young are born the following spring, the reproductive tracts of those females destined to produce young in the spring will show no macroscopic signs of pregnancy if the animals are killed in the fall and early winter. If the ovaries and uteri are histologically sectioned, inactive corpora lutea will be found in the ovaries and unimplanted blastocysts in the uteri (Hamlett, 1935, Wright, 1942). When histological examination of one of the first tracts obtained from a female wolverine showed corpora lutea and unimplanted blastocysts, it was decided to study reproduction as fully as possible in this species.

We are indebted to Drs. H. W. Mossman and C. H. Conaway who examined the slides, read the manuscript, and made numerous helpful suggestions.

MATERIALS AND METHODS

The wolverines examined by Rausch to date, more than 50 in number, have been secured largely through the cooperation of trappers. Never an abundant animal, the wolverine is continuously persecuted, and since July 1, 1953, the Territory of Alaska has paid a bounty on this animal. The animals were examined soon after death, or were frozen until examination was possible. After recording

Table 1. *Findings in female reproductive tracts of Gulo*

Date Killed	Weight of ovaries		Distribution of corpora lutea		Remarks
	Right	Left	Right	Left	
Oct. 18, '53	213	211	1	3	2 blastocysts, 1 dead embryo
Nov. 1, '51	113	152	2	2	1 blastocysts
Jan. '50	28	63			
Jan. '50	158	180	2	2	1 blastocysts
Jan. 20, '53	291	303	2	3	3 embryos, 1 resorbing embryo R, 3 L (22 mm. CR)
Jan. 25, '50	160	157			
Jan. 26, '53	107	110			
Feb. 2, '53	130	120	2	2	1 embryos, 2 R, 2 L, 2 ♂♂, 2 ♀♀ (68 mm. CR)
Mar. 21, '52	89	95			
Apr. 9, '53	202	199	4	0	Lactating; placental scars 2 R, 2 L
Apr. 10, '53	179	220	1	0	Lactating, placental scars 2 R, 1 L

appropriate measurements and other data, the animals were autopsied in order to collect internal parasites and other materials. The genital organs were fixed in 10 per cent formalin or A.F.A. The skulls and bacula were cleaned by dermestid beetles and bleached in hydrogen peroxide. All the skeletal material was handled uniformly. This report summarizes data from 22 males and 11 females obtained in northern Alaska from the fall of 1950 through the fall of 1953. The fixed reproductive tracts and the cleaned skulls and bacula were sent to Wright who studied the material.

Female tracts.—The ovaries were dissected free from the surrounding bursa, weighed to the nearest milligram, dehydrated in dioxan, infiltrated and imbedded in paraffin, and serially sectioned at 10 microns (Table 1). Representative sections were stained in hematoxylin and eosin or Groat's quadruple stain, and the slides studied. If corpora lutea were found in the ovaries of animals without macroscopically visible embryos, the upper third of the corresponding uterine horn was cut off, serially sectioned, and the sections searched for blastocysts. If blastocysts corresponding in number to the corpora lutea in the ovary were located, no further sectioning of that uterine horn was done. If all the blastocysts were not located in the first piece of uterus, the middle third was handled in the same way, and even the basal third was sectioned in some cases. Measurements were made of the corpora lutea and the blastocysts with an ocular micrometer and by counting the number of sections through which the structures extended.

Male tracts.—Each testis was dissected free of the tunica vaginalis, the vas deferens cut off close to the testis, and the combined weight of the paired testes and epididymides taken. A portion of one testis and the tail of the epididymis was cut out, sectioned, and stained. The presence or absence of sperm in both the testis and epididymis was determined.

Skulls and bacula.—Many of the usual cranial measurements were taken and

the skulls were studied for characters that might be useful in estimating age. After cleaning, the bacula were allowed to dry for several weeks and weighed to the nearest milligram.

OBSERVATIONS

Females. The female reproductive tract is typical of the Mustelidae. The ovary is enclosed in a bursa but there is an ostium out through which a portion of the fimbria extends. The uterus is bicornuate and the common lumen of the body is quite short. The fixed uterine horns in immature animals taken during the winter are about 60 mm. long by 3 mm. in diameter. In adults taken in fall or early winter the horns are about 90 mm. long and 5 mm. in diameter. No os clitoridis could be located macroscopically in the one adult vulvar region preserved.

The ovaries of immature females taken during the fall and winter months are without corpora lutea or large follicles. The cortical and medullary regions are distinct. The outer cortex shows many primary follicles and some medium sized follicles. The remainder of the cortex which comprises the largest portion of the ovary consists of large masses of interstitial gland cells, many of which develop from the theca of atretic follicles forming corpora atretica. Other cords of interstitial gland cells extend from the stroma of the tunica albuginea to the medullary stroma and these cells are probably derived from the stroma. The medulla is fibrous with numerous blood vessels and scattered clumps of small interstitial gland cells.

The ovaries of adult females taken during the fall and early winter tend to be somewhat larger than those of the immatures and they show inactive corpora lutea (Pl. 1). There are one to three corpora per ovary and they are from 1.65 mm to 2.00 mm in diameter on the stained slides. The corpora do not bulge from the surface of the ovary and they are not distinctly visible externally, but they could be seen easily macroscopically if the ovary were sectioned with a razor blade or sharp knife. The cells of these corpora are small, and in the November and January specimens are vacuolated like those seen in the corpora of winter killed marten (Wright, 1942). The cortical interstitial tissue is well developed in all three of the animals in inactive pregnancy and comprises the largest portion of the ovary. The medullary interstitial cells are especially well developed in the October specimen. They occur as scattered cords of large glandular cells. The October specimen shows some small follicles with antra and many corpora atretica, but the November and January specimens are without follicles with antra, and atretic follicles still showing degenerating eggs are extremely rare.

The ovaries of the two animals in active pregnancy are the largest (Pl. 1). Their corpora range from 3.38 mm. to 3.60 mm. and they are nearly seven times the volume of the inactive corpora of specimens taken earlier in the season before implantation. These corpora are very conspicuous externally in the intact ovary and some even appear to be attached to it by short pedicles only. The corpora are highly vascularized and show very large secretory cells without vacuoles.

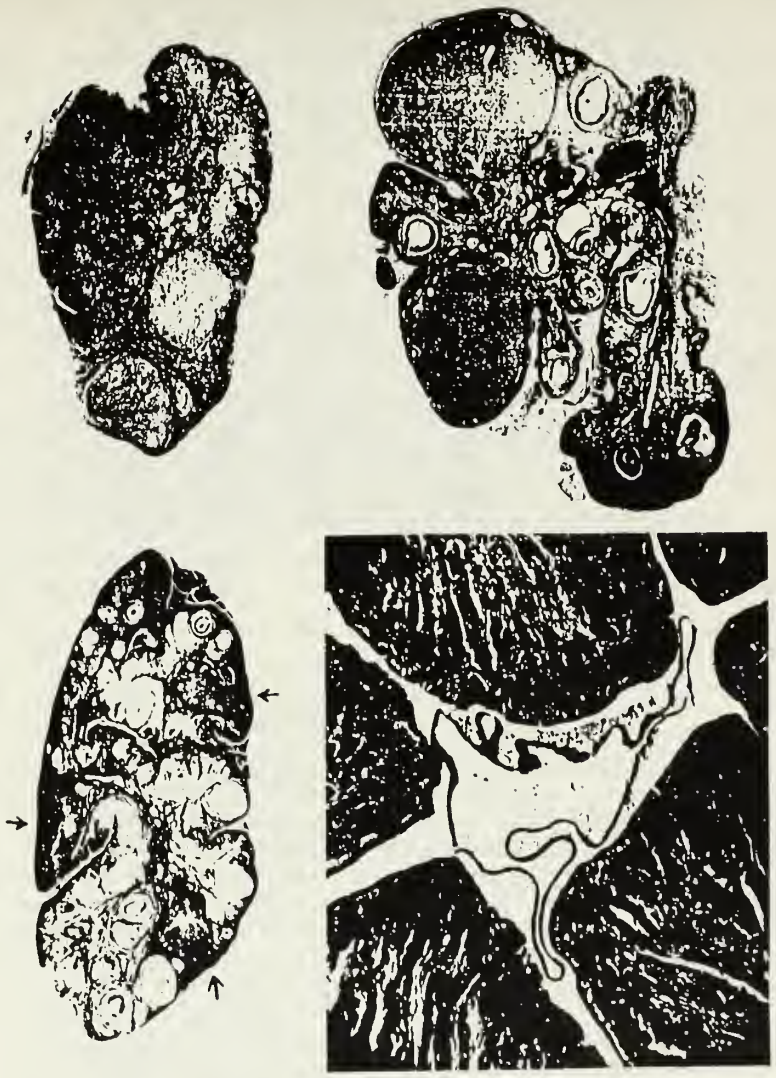

PLATE 1

Upper Left. Ovary of adult female with unimplanted blastocysts, showing two inactive corpora lutea. Animal killed in January. About 8.5 ×. Upper Right. Ovary of adult female with 68 mm. CR embryos showing two large active corpora lutea. Animal killed February 2. About 8.5 ×. Lower Left. Ovary of adult female during lactation showing three degenerating corpora lutea (shown with arrows) and absence of large follicles. Animal killed April 9. About 8.5 ×. Lower Right. Blastocyst of wolverine in situ in the lumen of the uterus. The conspicuous zona pellucida surrounds the embryo. Several nuclei can be seen within the embryo. From animal killed October 18. About 77 ×.

TABLE 2. *Summary of information on position, size, and numbers of cells in wolverine blastocysts*

Date Killed	Position of blastocyst	Dimensions in microns	No. of cells counted
Oct. 18, '53	Up. 1/3 L. U.	783 x 513 x 810	673
	Low. 1/3 L. U.	810 x 378 x 611	387
Nov. 1, '51	Up. 1/3 R. U.	1053 x 880 x 108	1021
	Up. 1/3 R. U.	1185 x 1120 x 189	987
	Up. 1/3 L. U.	1283 x 870 x 189	1077
	Mid. 1/3 L. U.	999 x 590 x 378	873
Jan. '50	Mid. 1/3 L. U.	615 x 159 x 202	47
	Low. 1/3 L. U.	1290 x 1013 x 1188	630
	R. U.	1188 x 940 x 189	980
	R. U.	1012 x 620 x 270	1513

The interstitial tissue has undergone considerable regression. There are numerous medium-sized follicles.

The ovaries of the two lactating females show degenerating corpora: in one case they are scarcely recognizable (Pl. I). These ovaries consist mainly of interstitial cell masses or corpora atretica. The interstitial cells are more numerous than in the active pregnancy stages. The lack of large follicles and the general inactivity of these ovaries makes it clear that the female wolverine does not have an estrous period shortly after parturition as has been reported for the fisher (Hall, 1942).

Placental scars could not be seen externally in the two tracts of lactating animals but when the uteri were bleached in hydrogen peroxide and dehydrated and cleared in methyl salicylate the ring-shaped scars could be seen distinctly.

The uterus of one of the animals with unimplanted embryos appeared somewhat larger and the macroscopic blood vessels were conspicuous. Histologically the blood vessels showed thick hyalinized walls and it is thought that this animal may have been parous.

Description of the blastocysts. Ten blastocysts were located in the three adult animals taken during the period of inactive pregnancy (Pl. I). The most conspicuous thing about these embryos is the heavy zona pellucida, about 7.8 microns in thickness, which can be seen even in the freshly mounted unstained ribbons. The embryos are lying completely free in the lumen of the uterus, and all are partly collapsed and some completely so. They are well enough preserved so that nuclear counts can be made but not well enough to distinguish between inner cell mass and trophoblast cells. They are similar to the blastocysts of field-preserved marten (Wright, 1942) but are larger and have more cells. Information on size, distribution, and cell counts is summarized in Table 2.

There is a great variation in the size of these blastocysts and in the number of cells of which they are composed. It is difficult to estimate their original size before collapse but they were probably about 2 mm. in diameter. The blastocysts may be at any position in the lumen of the uterus and the spacing of the embryos prior to implantation has not occurred in any of the animals. In the two lactating animals migration of some of the embryos from the right to the left uterine horn

TABLE 3. *Findings in male reproductive tracts of Gulo*

Date Killed	Weight of baculum	Estimated age	Paired combined weight of testes and epididymides	Presence of sperm
July 22, '52	462	Juv.	1775	None
Oct. 28, '51	1160	Im.	1713	None
Nov. 1, '51	2755	Ad.	1160	None
Nov. 1, '51	735	Im.	1365	None
Nov. 1, '51	Incomplete	Ad.	2098	None
Dec. 30, '51	1780	Ad.	1980	None
Dec. 11, '51	653	Im.		
Dec. 27, '51	1015	Im.	1698	None
Jan. 6, '52	1830	Ad.	3225	None
Jan. 19, '52	2175	Ad.	3325	None
Jan. 25, '52	1359	Im.	1075	None
Feb. 4, '53	2022	Ad.	8640	Spermatogenesis beginning, no sperm in epididymis
Feb. 21, '52	1175	Im.	3100	None
Feb. 28, '52	920	Im.	1645	None
Feb. 28, '52	2183	Ad.	1180	None
Mar. 25, '52	1373	Im.	1355	None
Mar. 26, '53	1215	Im.	3300	None
Mar. 31, '53	1158	Im.	5020	Few sperm in testis, none in epididymis
Mar. 31, '53	1009	Im.		
Apr. 1, '52	1129	Im.	6110	Few sperm in testis, none in epididymis
Apr. 4, '52	2910	Ad.	11070	Active spermatogenesis, some sperm in tail of epididymis
Apr. 16, '53	1212	Im.	2530	None

had occurred since all of the corpora lutea were in the right ovaries and placental scars were found in the left horns of both animals.

In two of the animals in inactive pregnancy a blastocyst was located for each corpus luteum. In the other, only two blastocysts were found although there were four corpora in the ovaries. In this case one small structure, 170 microns in greatest length, with distinct zona pellucida was found. There are small bodies within the zona which do not stain and it is thought that this is an embryo that died during cleavage. The other potential embryo was not located but it may have been lost if it were lying very close to one of the cuts made in preparing the uterus for imbedding.

The general picture of reproduction in the female wolverine can be seen from the data derived from the seven adult animals. Breeding takes place sometime between April and October, likely in midsummer. Development of the embryos is arrested when the blastocyst stage is reached and the embryos remain in this condition until January when implantation occurs. The young seem to be born in late March or early April. The number of young ranges from two to four. There may be loss of potential young prior to implantation or after implantation. Females apparently do not become pregnant during their first summer.

Males. The baculum of adult males is between 80 and 90 mm. in length (Pl. II). It is nearly straight but the distal end may be bent dorsally 15 or 20 degrees at about one-third of the way from the tip. The bone is round or oval in cross section and the base is enlarged somewhat. If viewed from the anterior end the tip is seen to be expanded into a three pronged inverted Y. In animals judged to be immature the bone is less massive and the basal end less well developed. Seven bacula from animals thought to be adults weighed from 1780 mg. to 2940 mg. and averaged 2338 mg., while 13 bacula from immature animals weighed from 653 to 1458 mg. and averaged 1134 mg. One baculum of the adult type had the tip cut off and was therefore not weighed. The baculum from a half-grown young obtained on July 22 weighed only 462 mg.

It is well known from the work of Deanesly (1935), Elder (1951) and Wright (1947) that the baculum of mustelids develops to full size only after the animal has reached sexual maturity, and Wright (1950) has shown that in *Mustela frenata* the presence of male hormone is necessary for maturation of the baculum. Accordingly those wolverines with small bacula are judged to be sexually immature.

The testes and epididymides of six adult and ten immature males taken during the fall, winter and early spring months were undeveloped and aspermatic (Table 3). Unmistakable evidence of sexual activity was seen in only four animals. An adult taken on February 4 with testes weighing 8640 mg. showed sperm production in the testis, but no sperm had reached the epididymis. An adult taken on April 4 with testes weighing 14,070 mg. was in active spermatogenesis and sperm were present in the tail of the epididymis. Two males considered immature on the basis of their bacula, taken on March 31 and April 4 were apparently just becoming active. A few sperm were in the testes but none in the epididymides. Probably full sexual activity would be found in adult males obtained in late spring or early summer. It is obvious that, since all males killed during November, December and January were without sperm, a winter breeding season can not occur in this species. At the time of implantation the males were sexually quiescent.

Skulls. The juvenile male taken on July 22, thus about four months old, had almost the entire lacteal dentition in place. All of the sutures were still open but the skull was already as large in several measurements as that of an adult female. The remaining skulls all came from animals taken in October or later and were thus from animals at least six months old. All of these skulls show the

TABLE 4. *Means of cranial measurements of wolverines*

Number and classification	Greatest length of skull	Condylobasal length	Zygomatic breadth	Post orbital processes	Post orbital constriction	Length of sagittal crest
7 ad. males	164.6	146.8	106.4	48.7	34.4	76.3
13 im. males	157.7	146.4	101.0	47.9	35.2	68.9
7 ad. females	147.8	135.8	97.8	46.5	33.4	62.4
3 im. females	144.4	131.9	94.4	43.4	33.4	55.0

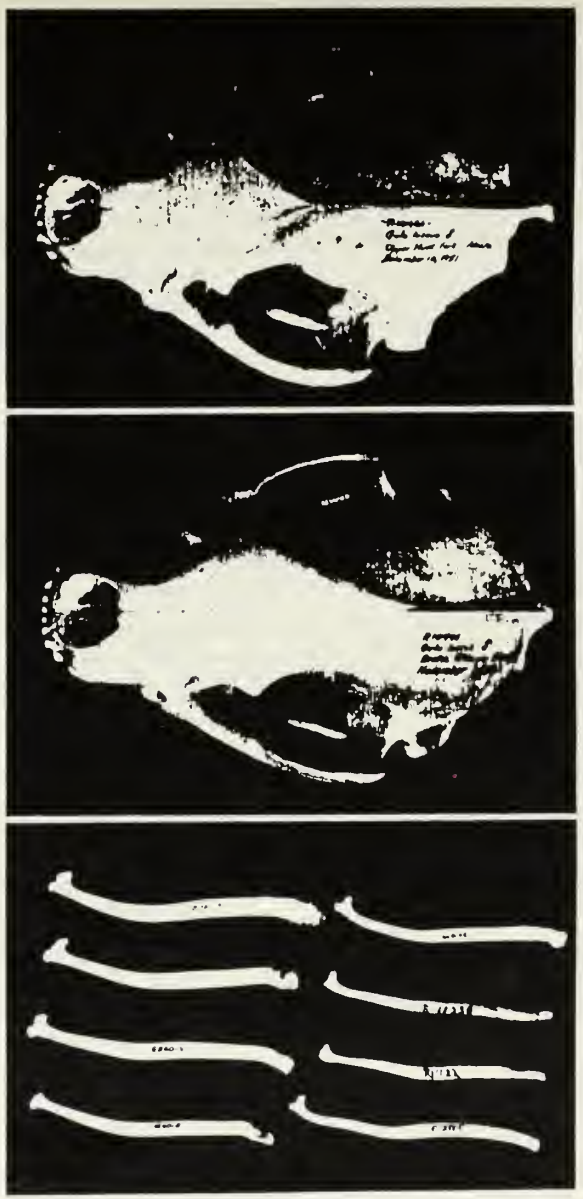

PLATE II

UPPER: Skull of adult male wolverine showing that all sutures have disappeared. The caudal extension of the sagittal crest is clearly shown. About ½ natural size. MIDDLE: Skull of immature male wolverine showing the internasal, naso maxillary, the naso frontal and the malar temporal sutures still open. The sagittal crest is less well developed than in the adult male. About ½ natural size. LOWER: Bacula of adult males on the left and immature males on the right. About ½ natural size.

great majority of the sutures to have disappeared, the permanent dentition is present and in males the sagittal crest is well developed (Plate II). Other writers such as Coues (1877) and Grinnell, Dixon and Linsdale (1937) have remarked about the rapid maturity of the skull in this species.

Means of measurements of the skulls were summarized according to sex and age in Table I, the immatures separated from the adults on the basis of the reproductive tracts. No one of the cranial measurements taken seems to be critical alone in distinguishing adults from immatures. It would appear that the longer sagittal crest in adult males might distinguish them from the immatures but the *t* test shows this difference is not significant. In adult males the sagittal crest seems to extend posteriorly further than in the immatures. A measurement of this character can be obtained indirectly by subtracting the condylobasal length from the greatest length of the skull. In seven adult males this averaged 11.9 mm. and in twelve immature males it is 11.6 mm. Although there is some overlap in individual cases, when analyzed by the *t* test the difference was found to be significant at the 5 per cent level suggesting that this is a real difference. The same situation is probably true in the females but the number of skulls is not large enough to permit the use of tests of significance.

All of the animals judged to be adults have all of the usual sutures closed. All the immatures taken in the fall and early winter have the malar-temporal, the internasal, and the naso-maxillary sutures still open. Some of the males with small baculа taken in March and April and thus judged to be about one year old have some or all of these sutures closed.

The degree of tooth wear does not seem to be of great significance in estimating age, especially since animals of both classes may show broken teeth partly caused by fighting the trap.

A ratio of eight adult males to 13 immature males was obtained and of seven adult females to only four immature females. In view of these different ratios of young to adults in the two sexes, one might ask if there were reason to suppose that the female wolverine matures a year earlier than does the male. A comparison of these ratios by the chi square method indicates that there is no reason to suspect this since the calculated value of chi square is not significant and ratios of eight to 13 and seven to four could be drawn from the same population with considerable frequency. Also the fact that only one type of skull appears in winter-killed immatures suggests rather strongly that there is only one age class of immature animals represented in this sample. It would logically follow that animals of both sexes mature during their second summer.

SUMMARY

The reproductive tracts of 22 male and 11 female wolverines taken mostly during the fall, winter, and early spring months in northern Alaska have been studied. Adult females taken in October, November, and January showed unimplanted blastocysts in their uteri and inactive corpora lutea in their ovaries. Ten blastocysts ranging in number from two to four per female were recovered. The blastocysts may have several hundred cells and they are about 2 mm. in diameter. A late-January and an early-February specimen had implanted embryos of 22 and 68 mm. crown-rump length respectively. Two early-April specimens were lactating but not pregnant. Four females were immature. The wolverine has a long period of gestation like many of the other mustelids. The breeding season is not precisely known but it probably occurs in mid-summer.

The baculum of the male is described. Immature males may be distinguished from adult males by their smaller baculа. The testes of males of both ages were largely inactive during the winter months. Full sexual activity was seen in only one male taken in early April.

The skull of the wolverine matures rapidly, but the young during the first year tend to show open sutures in the facial and zygomatic regions. The sagittal crests of first year animals do not extend as far posteriorly as do those of adults.

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